MODELLING GROWTH RESPONSES OF JUVENILE RADIATA PINE (*Pinus radiata* D. Don) CLONES SUBJECTED TO DIFFERENT WEED COMPETITION LEVELS IN CANTERBURY, NEW ZEALAND

BY

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TABLES OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

ABSTRACT

For a given site, species, genotype and management regime, tree growth is related to the amount, and temporal- and spatial-distribution of foliage, as governed by the prevailing below- and above-ground environment and intercepted photosynthetically active radiation. Canopy foliage budgets, therefore can provide first hand information about how trees cope with adverse environmental conditions and resource deficits in more subtle ways than height and diameter which are not as sensitive to changes in resource availability as leaf area. Process-oriented research, aimed at quantifying needle mortality within canopies and foliage growth dynamics of young radiata pine clones growing under varying competition gradients, therefore has the potential to improve decision tools for foresters charged with establishing tree crops.

During this study growth responses of juvenile radiata pine (*Pinus radiata* D. Don) clones to variable weeding micro-environments during the first 3 years after out-planting were evaluated. The study was established in a dry site on the Canterbury plains of the South Island of New Zealand. A complete randomised block design replicated three times in a split-plot layout was used. Four weeding treatments; 1) complete weeding, 2) 2 m diameter spots, 3) 1 m diameter spots around plants and 4) a control, formed the main plots while seven clones formed the sub-plots. Leaf area and specific leaf area spatial distribution as well as fascicle mortality in time and space were quantified. Annual crown foliage budgets of 3 of the clones were evaluated using regressions developed from limited destructive sampling and image analysis techniques. Changes in mean relative growth rate ($\overline{RGR}$) with tree size and age were evaluated by quantifying the morphological and physiological terms of the RGR expansion, to allow for changes in these terms;

$$RGR = ULR * SLA * LWR$$

where,

RGR = relative growth rate,

ULR = unit leaf rate,

SLA = specific leaf area and

LWR = leaf weight ratio.

Relative growth rate declined with tree age and size for trees in all weeded treatments but increased with age and size for trees in the unweeded control. The decline in RGR was mainly due to reduced ratio of dry matter turn over to leaf area i.e. unit leaf rate. Of tree age and size, size was the major factor influencing the decline in RGR. Of the 3 clones studied in detail, clone 3 had a different above ground carbon allocation strategy to clones 1 and 2, especially as regards leaf weight ratio and leaf area ratio.

Weeding influenced tree growth considerably. Significant clonal differences in height and basal-basal area were found. Trees growing in weed-free environments made favourable use of their micro-environments and significant genotype-by-weeding interaction was present for height. However, no "rich-kid" effect (some trees growing in weed-free micro-environments performing poorly) was found. Provisional models of height, basal-basal area and tree survival integrating weeding and clonal effects were also developed.

One of the significant findings from this study was the strong evidence against the constant RGR model which has been used by many researchers of tree growth analysis. The results further demonstrated that trees growing with weeds were predisposed to perform poorly due to reduced canopy production as well as having higher proportions of older, less efficient foliage.

The results from this study lay the framework to explicitly quantify clonal responses to resource deficits arising from management inputs using variables directly involved in canopy production (i.e. leaf area).

CHAPTER 1

INTRODUCTION

1.1 GENERAL INTRODUCTION

In plantation forestry, the first five years of growth following out-planting are crucial to the success of most forestry ventures (Evans 1992, Belli 1987, Payandeh 1987, Belli and Ek 1988). Correct silvicultural and management decisions for example, species and provenance choice (Evans 1992, Burdon 1995), stock type and quality (Chavasse 1980, Trewin and Cullen 1985, Menzies 1988), genetics (Shelbourne 1986, Burdon 1995), land preparation (Mason and Cullen 1986), planting quality (Mason 1985) and timely release from competing vegetation (Walstad and Kuch 1987, Wagner *et al.* 1989, Evans 1992, Mason 1992, Richardson 1993, Mason and Kirongo 1999, Willoughby 1999, Zutter *et al.* 1986, Zutter *et al.* 1999a,b, Richardson *et al.* 1999), made at this early age have profound influences on the future growth, survival, harvest volumes and profit margins (Mason 1992, Mason 1996, Payandeh 1987, Belli and Ek 1988). This study evaluated the growth responses of juvenile radiata pine (*Pinus radiata* D. Don) clones, growing on a dry site in the Canterbury plains of the South Island, New Zealand, to varying gradients of weed competition.

The New Zealand plantation forestry estate covers 1.7 million hectares or 6 % of the total land area. Radiata pine constitutes 90.5 % or 1.52 million ha (Burdon 1995, New Zealand Official Year Book (N.Z.O.Y.B.) 1998, New Zealand Forest Owners Association (N.Z.F.O.A) 1999). Current afforestation rates are 63 000 ha with a further 28 000 ha of restocked land (Burdon 1995). This means that a third of the total resource is in the juvenile age bracket (N.Z.F.O.A. 1999). Radiata pine's prominence in the New Zealand forestry scene is due to the following reasons:

1) fast growth rates - New Zealand radiata pine has one of the highest mean annual increment rates (24 m^3/ha/yr) in the world;

2) excellent response to silviculture and management manipulations;

3) advanced research programs to support and foster plantation development (Purey-Cust and Hammond 1995); and

4) versatility and ability to grow in many sites giving suitable timber for many uses (Maclaren 1993, Cown 1992).

With such a vast resource contributing significantly to the Gross Domestic Product (3.9 %) (N.Z.F.O.A. 1999) and foreign earnings, it is imperative that the management guidelines be set on a firm, well researched footing. For example, the export of forestry products earned New Zealand $2.831 billion for the year ended March 2000, which accounted for 12.2 % of total exports (MAF 2000). Forestry was the 3rd largest export earner for the year ended 1997 (N.Z.O.Y.B. 1998). Research on various aspects of radiata pine, from genetic improvement to silviculture and management is quite advanced in New Zealand. "State-of-the-art" growth and yield models have been developed commensurate with management needs. This notwithstanding, frequent reviews and/or improvements to existing approaches and models are necessary, from time to time, so that new knowledge can be appropriately integrated into management decision frameworks. Moreover, with the increased use of genetically improved planting stock (Burdon 1995) and the changes in global weather patterns, models developed from past records may incur some considerable bias if applied to current crops in the field.

Forest managers want to have quantitative indicators of tree survival and performance given a set of site modification procedures, silvicultural manipulations and stock type to meet desired management/end-user goals (Mason 1996). Genetics and the interaction between genotype and site modification (e.g. weed control intensities) need to be explicitly expressed in growth and yield models of juvenile crops so that managers can choose appropriate clones for their sites. This is very important especially bearing in mind that weeds, for example, are one of the most significant causes of economic losses and environmental damage in agriculture and forestry systems in the world (MacFadyen 1998).

Models of juvenile growth of radiata pine in New Zealand have been developed by Mason (1992) and Mason and Whyte (1997) for the Central North Island and Zhao (1999) for Canterbury in the South Island. However, both Mason (1992) and Zhao (1999) had limited data with respect to intensity of weeding treatments and genetic effects. Models sensitive to the variety of weeding intensities which managers tend to use in practice will be of immediate use to managers. On the other hand, growth gains from genetics have been reported to manifest themselves after the juvenile phase (e.g. Shelbourne 1986, Burdon 1995) and models incorporating genetics and genotype-by-weeding interactions will provide much needed information (e.g. starting coefficients) for use in models of mature stands.

Above-ground tree growth is affected by numerous within-tree processes and external factors. Thus, although height and diameter are of major interest to foresters because they give estimates of volume or fibre present, they are not driving variables in the growth process. The amount of various age classes of foliage and their distribution within the canopy influences light absorption and C-fixation (Woodman 1971, Watts *et al.* 1976, Leverenz *et al.* 1982, Wang and Jarvis 1990, Kinerson *et al.* 1974, Landsberg 1986, Charles-Edwards *et al.* 1986, Grace *et al.* 1987a,b, Xu 2000). Consequently, better insights into the ways trees cope with resource scarcity and use resulting from management inputs and/or modifications of the growing environment may be achieved by direct measures of foliage growth and canopy dynamics. Therefore, process-oriented research aimed at quantifying foliage growth dynamics, needle mortality within canopies and at estimating crown foliage budgets of young radiata pine clones growing under varying weed competition gradients could contribute to the development of forester's decision tools.

Pertinent questions to be objectively addressed in the study described here were:

1) how do young radiata pine clones' annual crown budgets change with varying competition levels?
2) are reductions in growth, frequently observed in competition studies, the result of reduced amounts of new foliage the trees can produce? Are these reductions in canopy production directly related to changes in environmental variables such as soil water?

3) how do different radiata pine clones respond to varying competition gradients? and

4) are changes in total needle surface areas related to competition gradients and/or genotype? Moreover, are these changes in total needle surface areas reflected by variation in specific leaf areas in different crown parts and/or different needle ages?

Additionally, given that models of young crops require a decay in relative growth rate (RGR is the ratio of growth to size at the beginning of the growth period) with size and/or age, can studies of canopies help explain this phenomenon?

Answers to these questions are important if we wish to understand the underlying mechanisms of inter-specific competition in juvenile plantations. The findings presented in this thesis are derived from of an intensive study on a genotype-by-weed competition experiment designed to address the objectives set out in the next section.

1.2 STUDY OBJECTIVES

In this study the following principal hypotheses were investigated.

1. H_{01}: Annual crown foliage budgets in young radiata pine are functions of tree age/size, varying weed competition levels, genotype and/or their interaction.
2. H_{02}: Decrease in RGR with time and/or tree size in young crops which are free-growing (prior to between-tree competition) is due to changes in the terms of the relative growth rate (RGR) expansion.
3. H_{03}: The "rich-kid" effect (some trees growing in weed free environments performing poorly) is the result of genotype-by-weed competition interaction.

The general objectives of this study were as follows.

1. Use image analysis, fascicle monitoring techniques and limited destructive sampling to estimate annual crown foliage budgets in young radiata pine as functions of tree age/size, varying weed competition levels, genotype and/or their interaction.
2. Estimate terms in the relative growth rate (RGR) expansion to try to explain why RGR diminishes with time and/or size in young crops which are free-growing (prior to between-tree competition).
3. Determine whether or not the "rich-kid" effect (some trees growing in weed free environments performing poorly) is a result of genotype-by-weed competition interaction.
4. Develop provisional models of juvenile radiata pine tree growth and survival incorporating varying competition gradients and genetics to assist managers who need to make informed decisions about weed control systems and clonal selection.

1.2.1 Specific objectives

The specific objectives of the study were as follows.

1) Use image analysis and limited destructive sampling to estimate total crown foliage amounts and total tree biomass.

2) Quantify needle mortality as a function of needle age, time, crown position, tree size, genetics and competition intensity.

3) Hence, from 1 and 2 (above), estimate annual crown foliage budgets as functions of tree size, genetics, competition and their interactions.

4) Quantify seasonal foliage growth dynamics especially, needle growth and leaf area spatial distribution within the crowns of *Pinus radiata* and relate these to genetics and competition gradients.

5) Aid understanding of why RGR diminishes with time and/or size by quantifying unit leaf rate (ULR), specific leaf area (SLA) and leaf weight ratio (LWR) terms of the RGR expansion;

$$RGR = \underbrace{\frac{dW}{dT}\frac{1}{LA}}_{ULR} * \underbrace{\frac{LA}{Lw}}_{SLA} * \underbrace{\frac{Lw}{W}}_{LWR} \qquad (1.1)\ \text{(Evans 1972).}$$

where;

LA = leaf area, LW = leaf dry weight, W = tree dry weight and

dW/dt = change in dry weight over time.

Outputs from 3 and 4 (above) were used to estimate the RGR terms.

6) Test the hypothesis that the "rich-kid" effect reported by other researchers (e.g. Wagner *et al.* 1989, Kirongo 1996) is a result of genotype by weed competition interaction.

7) Develop provisional models of juvenile radiata pine tree growth and survival incorporating genetics and varying competition gradients.

1.3 SCOPE OF THE STUDY

The data used in this study came from a 3-year-old weeding by clone experiment. The species studied was radiata pine (*Pinus radiata* D. Don). The site was dry (600 mm average annual rainfall). The soils were Lismore stony silt loams. Grasses, especially Italian ryegrass (*Lolium multiflorum*) and other non-crop vegetation, in particular white clover (*Trifolium repens*) and sorrel (*Rumex acetosella*) were the main competing vegetation. The models and general findings reported here are relevant to crops of similar species and age and grown under similar conditions. Extrapolation to other sites or conifer species, or to radiata pine of older ages or different genotypes may give biased results. Weather variables may also lead to differences in growth trends from year to year and this should also be taken into account when using the findings.

CHAPTER 2

REVIEW OF RELEVANT LITERATURE

2.1 PLANTATION ESTABLISHMENT

2.1.1 Overview

Evans (1992) defined plantations as large expanses of artificially planted trees displaying "orderliness and uniformity" of spacing, tree age and species with characteristic "regular shape and distinct boundaries". Further, Evans (1992) distinguished afforestation (new planting on land that has never had forest) from reforestation (replanting of harvested land with the same or different species within 5 decades of harvesting).

The objectives of plantation establishment differ markedly depending on the country/region (e.g. developed vs the less developed nations), site characteristics, available resources, social-economic and -political environment as well as the life style of the populace. Thus for example, in most developing countries, in addition to serving the common goals of timber provision and wood sustenance, climate amelioration, carbon sequestration and protection of fragile ecosystems, plantations are a source of much needed wood fuel for domestic (cooking and heating) and small industry use (e.g. pottery) (Evans 1992). In most of these regions plantations serve a profound ecological function by diverting pressure from already devastated and dwindling natural vegetation while at the same time improving the livelihood of the people (Evans 1992), especially rural folk. However, perhaps the main drive behind massive plantation ventures in many countries is the associated economic gains from the sale of wood fibre (Westoby 1987). In a contribution to plantation establishment practices in New Zealand, Viles (1981) noted that the decision 'to plant or not to

plant' needed to include a proper evaluation of not only site factors, risk and financial returns but also the social, environmental and legislative aspects.

In this chapter some of the important elements for successful establishment of radiata pine in New Zealand and in particular genetics and weeding are highlighted. A brief discourse on clonal forestry and its advantages and challenges is presented. Plant growth analysis and growth and yield modelling are also discussed.

2.1.2 Objectives of plantation establishment

In New Zealand, forest managers establish plantations of radiata pine with the main goal of growing a healthy uniform crop so that they can harvest optimum volumes and/or weight of fibre and as a result maximise net returns at the end of the rotation. In order to realise this, final crop trees of reasonable size (diameter and height), and of acceptable form with minimum or no stem defects must be raised (Mason 1992, Maclaren 1993). Commercial forestry of intensively managed monocultures therefore has the following main aims:

1) to promptly establish forests in new areas;
2) to reforest felled sites with fully stocked stands, and
3) to maintain reasonable stock with sufficient vigour to assure harvests within a reasonable time.

The characteristics of final crop trees can be influenced by numerous natural events, however, for example, the inherent ability of the sites to grow trees fast, favourable weather, absence of catastrophes especially windthrow, diseases and pests. Meanwhile, management and silvicultural inputs (e.g. site preparation, weed control - Lanini and Radosevich 1986, Mason 1992) if well tailored can also enhance growth and form acceptability of the final crop trees. The genotype of the stock can also enhance growth and form (Burdon 1995).

The "Establishment phase" or "Early or Initial growth phase" (Mason 1992) is a term used normally to describe the events between planting and crop canopy closure

(usually age 5 for radiata pine in New Zealand). It is increasingly being appreciated that the establishment phase is a very crucial and important phase in the growth of forest crops (Belli and Ek 1988, Sutton 1991, Mason 1992), when many of the future growth trends of the crops can be imparted. The significance of this phase and its contribution to the future of the crop is well summarised by Sutton (1991):

> "*.. we can have the best genetic material and the best regime but it is all for naught unless we get the trees established ..*"

The qualitative as well as quantitative understanding of the effects of silvicultural and management manipulations on the future of the crop is an important prerequisite for successful regeneration (Belli and Ek 1988). Moreover, quantitative models of the inter-relationships between site factors, stock type and quality, genetics and costs (Payandeh 1987) can help ensure establishment success. This is evidenced by the current trend in New Zealand, for example, whereby improved establishment practices have resulted in reduction of the number of seedlings planted per hectare (now about 800 compared to 1600 in the past) (e.g. Mason 1992).

2.1.3 Important elements of successful establishment

Successful establishment depends on a number of interacting factors especially pre-plant and immediately post-plant factors (Mason 1992). It starts with selecting the correct species and provenance (Evans 1992) for the site and using quality planting material of improved genome (Shelbourne 1986, Burdon 1995). Pre-plant factors that can adversely affect tree growth and survival include harvesting practices (Compton and Cole 1991, Dyck *et al.* 1991, Senyk and Smith 1991), site preparation techniques (Skinner *et al.* 1989, Balneaves *et al.* 1991, Senyk and Smith 1991) and nursery production regimes (Knight 1981, Mason 1981, Sutton 1991). Balneaves *et al.* (1991) reported root raking and/or burning of slash during site preparation to result in nutrient losses which affected tree establishment and growth. Skinner *et al.* (1989) found removal of litter and slash created temperature and moisture regimes unsuitable for good tree establishment. Senyk and Smith (1991) found mixed effects

of harvesting and mechanical site preparation methods, however. They noted that soil characteristics were important in determining the magnitude of the impacts.

The important factors with regard to nursery production systems are control of diseases and insect pests (Ray 1981, Kay 1981), weed control (van Dorsser 1981a) and seedling quality (Bowles 1981, Rook and Menzies 1981). The morphological and physiological quality of seedlings (Menzies *et al.* 1981, Rook and Menzies 1981) can be favoured by conditioning (van Dorsser 1981b, Brunsden 1981a, Sutton 1991), seedling spacing in the beds (Bowles 1981) and weeding (van Dorsser 1981a). Sutton (1991) reported an 18 months height advantage by age 4 for undercut, wrenched stock compared to stock which had not been conditioned. Sutton stated further that faster growth was also accompanied by a reduction in branches per unit stem length which translated to reduced pruning costs.

Meanwhile, field preparation and cultivation (Cullen and Mason 1981) for example land clearing, mounding and discing in difficult soils (Hunter 1981, Mason and Cullen 1986) is important. Proper handling of the planting stock i.e. lifting, packaging and transportation (Balneaves and Menzies 1990, Mason 1985) and planting quality (Jackson 1981, Trewin 1981, Mason 1985) can enhance root development and increase growth and survival of planted seedlings (Hunter 1981, Jackson 1981), while at the same time reduce toppling (Brunsden 1981b). Harris (1981) reported that toppling encouraged formation of reaction wood thus lowering wood quality. Beating-up or blanking (replacement of dead trees) results in lost opportunity if it is not done within a few months of initial planting as replaced trees may never 'catch-up' to form the main crop (Chavasse 1981). Poor survival leading to blanking increases establishment costs. It is therefore important that all planted trees survive.

Post-plant treatments are for example fertilization (West 1981, Squire 1977) and especially weed control (Balneaves 1981, Sands and Nambiar 1984, Walstad and Kuch 1987, Smethurst and Nambiar 1989, Wagner *et al.* 1989, Evans 1992, Mason 1992, Richardson 1993, Wagner and Radosevich 1991a, Kirongo 1996, Zutter *et al.* 1999b). Good husbandry following out-planting is very important to ensure the

invested effort and resources pay off and that most of the trees qualify for selection as final crop trees. Managers therefore, need to view the establishment phase as continuity of inter-related processes which not only impact on the growth and survival but also on future stand operations, costs and harvestable volumes (Sutton 1981).

From this brief discussion, it is evident that the establishment phase is a time when managers can improve future growth rates and increase crop profitability. Managers are better placed to take full advantage of this phase provided they have the correct information in a readily usable form (Mason 1996, Mason and Whyte 1997).

2.1.4 Long-term responses to establishment practices

The effects of establishment practices in the long-term, need to be quantified and appropriately integrated in to growth models (Mason *et al.* 1997). This will ensure that managers have quantitative estimates of the costs and benefits of various establishment procedures. One way of achieving this goal is to incorporate malleable terms into present growth and yield models to represent observed long-term growth effects (Mason *et al.* 1997, Pienaar and Rheney 1995). For this to be achieved observations over the full rotation of various establishment practices need to be made. Emphasis should be placed on understanding the processes driving plant growth and how these are modified by managerial inputs (Mason *et al.* 1997), including the inter-relationships between site and environmental factors, vegetation control, water and the supply and use of nutrients (Powers and Reynolds 1999). This is especially necessary given that shifts in significance of treatment and/or stock type effects can occur after the establishment phase (McDonald *et al.* 1999). The experiment used in this study will be maintained to full rotation to provide first-hand information on rotation-length effects of establishment practices.

Snowdon and Waring (1984) and Snowdon and Khana (1989) hypothesised two types of long-term growth responses to establishment practices. Response type I was a short-term gain (parallel growth trend) between treated and untreated crops with

growth patterns returning to normal trends soon after. Response type II was characterised by an increasing growth difference (divergent trends) between treated and untreated crops which was sustained (Figure 2.1).

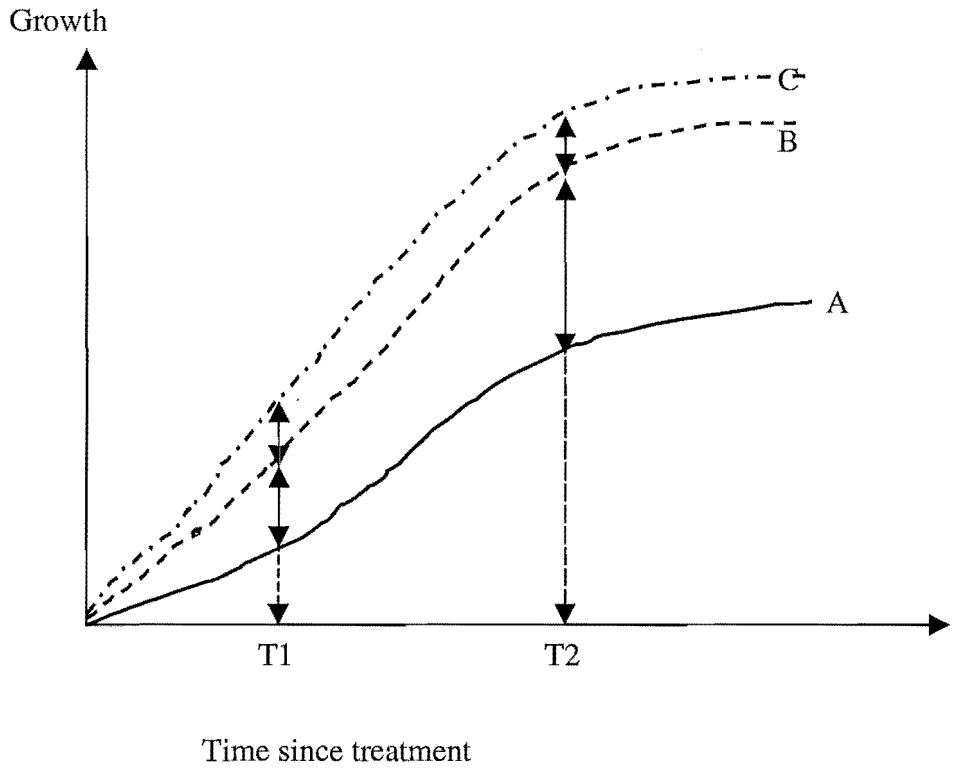

Figure 2.1: Hypothetical type I (B &C) and type II (A&B, A&C) responses. Double-headed arrows show increasing divergence from T1 to T2 between A&B and A&C, but parallel trends between B&C.

Woollons *et al.* (1988) reported type I responses to fertiliser application in 3 out of 4 experiments. Other researchers who observed type I responses are for example Mason *et al.* (1988) for soil cultivation, Mason *et al.* (1997) for mounding, Mason *et al.* (1997), Snowdon and Waring (1984), Snowdon and Khana (1989) and Mason and Milne (1999) for weed control. Mason and Milne (1999) found a type II response after fertilisation at one site where site preparation methods included moving of top soil and slash into mounds, while Snowdon and Waring (1984) reported a similar response after fertilization. Powers and Reynolds (1999) reported initial advantages

from weeding to decrease as trees closed canopy and in moving from low to high quality sites in a ten-year study on ponderosa pine.

Mason (1992) suggested that for the response types I and II to be easily investigated researchers needed to compare growth trends based on time gain rather than on yield basis.

2.2 GENETICS

2.2.1 Improved breeds and clonal forestry in New Zealand

Radiata pine constitutes over 90.5 % of the plantation area in New Zealand (Shelbourne 1986, Burdon 1995, N.Z.O.Y.B. 1998, N.Z.F.O.A. 1999). With such a large investment, the provision of genetically superior material is crucial to ensure continued success. Material of low genetic quality can result in low productivity and financial losses as was evident with *Pinus ponderosa* and *P. nigra* planted in the 1920s in New Zealand (Shelbourne 1986, Burdon 1995).

The New Zealand Forest Research Institute Ltd (Forest Research) has been running a breeding programme for radiata pine since the 1950s (Burdon 1995). This programme was intensified in 1987 with the Forest Research and Industry co-operative initiative aimed at intensive genetic improvements while at the same time maintaining genetic diversity to ensure long-term flexibility. Radiata pine seed was collected from areas with similar latitude and climate to the main growing sites in New Zealand. The selection was however, limited to 3 native populations in California. Most of the current seed of radiata pine in New Zealand is a hybrid mixture of the Ano Nuevo and Montrey populations. The other native sources are Cambria, Guadalupe islands and Cedros islands. Of these 3 latter sources, the Guadalupe is the most promising (Burdon 1995).

Breeding in New Zealand took the following 3 steps (Burdon 1995).

1) Genetic resource population - seed from the full range of native countries for *P. radiata* was used to set up provenance trials. These provenance trials were later used to provide stock for future breeding work. All 5 native populations of radiata pine were represented.
2) Breeding population - pure-bred or pedigree full-sib families (300 or more genotypes) were raised to provide sources for future selection. Selection and crossing of "best" individuals in each generation resulted in better offspring at each progressive step.
3) Seed production population - this is the highest level in the breeding hierarchy. Rigorously tested genotypes were used to set up clonal seed orchards. Sixteen or more unrelated parents were used to ensure significant genetic diversity.

Selection mainly concentrated on certain important traits especially fast growth, bole straightness, even and multinodal branching, reduced forking, and disease resistance. Shelbourne (1986) reports gains of 20 to 30% in volume and 25% improved bole straightness, 65% multinodal branching and 13% malformation score to be characteristic of the 268 and 875 series at age 4 to 6 years.

2.2.2 Seed orchards

Seed orchards were first set up in New Zealand in 1958. These were mostly open-pollinated i.e. the source of pollen was not known. In recent times control-pollinated hedged orchards have been used. These orchards combine intensive selection with the fact that the pollen source is known with the end result that high performance stock is produced. The genetic constitution of the seed lot is chosen to augment desired features, for example resistance to *Dothistroma pini* and *Cyclaneusma* spp., growth and form as well as good adaptation to sites (Burdon 1995). Cuttings from stool plants raised in the nursery are used to multiply the superior clones. This method is cheaper than raising the plants directly from seed because the cost of individual seeds makes multiplication through cuttings cost-effective. The superior characteristics in the improved genotypes start to become evident after the juvenile

phase (first 5 years for New Zealand radiata pine) and continue to be more apparent as the stands mature (Shelbourne 1986, Burdon 1995).

In New Zealand there are 3 main classifications of seedlots (Genetics and Tree Improvement Research Field 1987, Burdon 1995).

1) Growth and form (GF) - the higher the GF rating the higher the growth rates and final volumes harvestable. The trees also show a wide range of adaptability with much less malformation.
2) Long-Internode (LI) - this refers to the distance between branch whorls. Long internodes result in reduced intensities of pruning and clearer lumber.
3) *Dothistroma* resistance (DR) - seed from control pollinated seed orchards is used as the source. Trees show reduced incidence of *Dothistroma* attacks. Control pollinated seed is superior to climbing select or bulk seed.

2.2.3 Family forestry versus clonal forestry

2.2.3.1 Definitions: what is a clone?

The use of clones dates back to the early part of the 19th century when European horticulturists used grafting methods (Ahuja and Libby 1993b). The concise Oxford dictionary (1995) defines a clone as "*a group of cells or organisms produced asexually from one stock or ancestor*". In forestry clones are genetically identical trees produced asexually from seed material (cotyledon or embryo) or vegetative tissue of genetically identical parent. Ahuja and Libby (1993a) gave 3 definitions of a clone; 1) plants produced asexually from cuttings or grafting, 2) "*cell lines from different single cells of the same organism*" and 3) modified plants resulting from the introduction of foreign DNA or gene(s) using modern biotechnology methods.

Clonal forestry on the other hand, is defined as *the* "*establishment of forest plantations using tested clones*" and contrasted from family forestry which is the "*vegetative multiplication of mixtures of controlled-cross progeny from among the best general combiners*" (e.g. Tombleson and Carson 1991, Ahuja and Libby 1993a,b). It should therefore, be clear that the use of clones in a planting programme

does not necessarily imply clonal forestry, rather the massive use of tested clones of proven performance and showing high within clone uniformity (Ahuja and Libby 1993a).

2.2.3.2 Methods for the mass production of improved material

Various methods are currently used for the mass propagation of improved scarce seed and/or vegetative material. Some of the methods used for multiplication of scarce seed or plantlets, for example organogenesis, are NOT cloning methods in the strict sense of the term (Walter *et al.* 1997).

Two methods of mass production of scarce seeds or propagules commonly used are organogenesis and embryogenesis (Walter *et al.* 1997). Of the two, embryogenesis is a mass propagation method as well as a cloning technique. Genetic engineering is a cloning technique used to "improve" the genome of an individual by introducing useful traits (Ahuja and Libby 1993a, Walter *et al.* 1997, Mullin and Bertrand 1998). Walter *et al.* (1997) defined organogenesis, embryogenesis and genetic engineering as follows:

1. Organogenesis - this method involves the initiation, elongation, multiplication and rooting of shootlets in sterile medium (Agar). The plantlets are thereafter transferred to stool beds in nurseries where they can be multiplied using appropriate methods e.g. cuttings.
2. Embryogenesis - undifferentiated embryonic tissue is multiplied and grown in to mature embryos from which normal (somatic) seedlings result. The embryonic tissue is usually from young immature cones.
3. Genetic Engineering - genes from other organisms are used to "carry and introduce" valuable traits into an individual. The foreign DNA integrates into the recipient's genome.

Genetically engineered plants have been called 'transgenic', or 'bioengineered'. Mullin and Bertrand (1998) defined a transgenic plant as one that had "new DNA sequences introduced by recombinant DNA techniques". Further, Mullin and Betrand (1998) named two forms of genetic transformations arising from; 1) use of living organisms as the carriers of the foreign genes or DNA and are called biological

transformations and 2) physical transformations involving non-living organisms as in particle bombardment e.g. "microprojectile-mediated transformation".

Genetic engineering protocols for herbicide resistance of bio-degradable chemicals as well as for resistance to some pathogens are at an advanced stage for radiata pine in New Zealand (Walter *et al.* 1997).

2.2.3.3 Advantages of clonal forestry

In discussing the advantages of clonal forestry and putting these into proper context it is important to contrast cloning techniques with clonal forestry. Cloning techniques are the methods used to produce clones, for example embryogenesis, while clonal forestry denotes the use of tested clones in plantations. While some authors have expressed differences of opinion regarding the perceived and actual benefits of clonal forestry (cf. family forestry) especially regarding the costs associated with clonal forestry (e.g. Tombleson and Carson 1991), it is increasingly becoming evident, however that clonal forestry has a number of unique benefits which it can offer the forest and other related industries.

In New Zealand, the future of radiata pine clonal forestry looks bright especially after earlier hurdles like poor rooting and optimal physiological age of propagules were surmounted (Menzies *et al.* 1991, Shelbourne 1991). Maximum benefits from clonal forestry will depend not only on the use of superior material but also correct matching of clones to sites (Olsen 1997, Shelbourne 1997, Cown *et al.* 1991, Carson and Inglis 1988). Additionally, embracing "genetics of value adding to the end products" as one of the goals can enhance profitability immensely. This is where breeding for specific end-user traits (e.g. stiffness, stability during drying, inter-node length, resin pockets and face-appearance) rather than for growth rates and volume production per se is used (Shelbourne 1997, Shelbourne *et al.* 1997). The possibility of using "GFPlus" certificates will ensure that only tested and certified material finds its way into the markets (Shelbourne 1997).

Recent research break-throughs plus the availability of superior families, added to better data storage and retrieval systems, have contributed to sound cloning

techniques (Ahuja and Libby 1993b). Libby and Rauter (1984), Carson and Burdon (1991), Ahuja and Libby (1993b) and Shelbourne (1997) summarized the main arguments in support of using clones as opposed to classical tree improvement procedures. In embracing these advantages it should be borne in mind that many of these points refer to the actual mass production of clones and not to "clonal forestry" per se. As Carson and Burdon (1991) observed, some of the advantages of "clonal forestry" bear close resemblance to those of "family forestry" using improved control-pollinated seed.

1. Clones can easily and cost-effectively be multiplied using tissue culture or organo-genesis and embryogenesis techniques. The costs of production using traditional tree breeding methods are prohibitive. Moreover, controlled pollination may result in incompatibility and reduced percent viability of embryos. Cloning of embryos or seedlings using effective biotechnology techniques for mass production (Walter *et al.* 1997) can resolve this problem.

2. Clones are more amenable to improvement through research as a few genes can be selected during breeding and then enhanced to meet end-user defined goals. This can be achieved without necessarily narrowing the genetic diversity. Clonal programmes use a diverse genetic base from which to select. Moreover, previously discontinued clones can easily be re-incorporated into future programmes unlike in classical tree breeding where seed orchard representing only a few parents are used to procure seed for vast afforestation/reforestation ventures.

3. Better cloning techniques can be used to capture non-additive variation (offspring performance not similar to parents, cf. Additive variation where offspring performance is similar and can be predicted from parents). Thus, poor perfoming clones can be removed from orchard material by identifying favourable genes and breeding selectively to favour these genes. Alternatively, superior genes can be introduced using genetic engineering techniques to enhance the mediocre genes.

4. Clones are less susceptible to diseases which arise due to inbreeding (selfing with close neighbours as might happen in a seed orchard), for example susceptibility to abiotic and biotic stresses that occur later in life.

5. There is considerable shortening of the time from selection to mass production of desirable clones compared to traditional tree breeding procedures. However, Tombleson and Carson (1991) contend that maintenance of juvenility and a possible lag phase of about 10 years during testing may erode this advantage.

6. It is cheaper in the long-run to operate clonal programs as the single clone is the unit of management unlike in seed orchards where all the trees in the orchard serve as the unit of management.

Other advantages include the potential to improve wood production by reducing reproductive activity of clones. Managers can use clones designed to perform best in their regions (Cown *et al.* 1991, Carson and Inglis 1988) with known safety margins against disease or insect attacks (Libby and Rauter 1984). Clones can also be effectively used as "correlation breakers" for negatively correlated factors, for example wood density vs diameter growth rate or inter-node length and diameter growth vs stem form (Shelbourne 1997). Choosing clones with above average performance for the desirable traits and improving on these can alleviate this problem (Libby and Rauter 1984).

Given all the aforementioned advantages, it is important to note however, that clonal forestry has some potential drawbacks. Burdon (1999) argues that while the introduction of foreign genes into an organism through genetic engineering to modify its genome and thereby increase desirability is of benefit, researchers need to develop parallel methods of risk management. Of particular concern are likelihood of contamination of non-target populations (e.g. through wind pollination) or the possibility of weeds becoming resistant to chemicals and diseases (e.g. Mullin and Bertrand 1998). Target trees may also develop in ways not envisaged earlier. Burdon (1999) specifically singles out *"..adverse side effects of transformation on crop fitness"* to be a real issue warranting discussion and preparedness on the part of

researchers in genetic engineering. In their contribution to the problems of clonal forestry, Ahuja and Libby (1993a,b) cited biological (e.g. the question of genetic diversity), economic (prohibitive initial costs) and ethical (playing God) problems to be viewed as "challenges to be met" through continued research and testing of pedigreed clones. Better public relations will also help immensely in dissipating many of the unfounded fears associated with genetically modified organisms.

In summary, embracing clonal forestry can have the following perceived benefits to the New Zealand forestry industry (Burdon 1995, Shelbourne 1997, Shelbourne *et al.* 1997, Carson and Burdon 1991):

1) improved growth rates and hence reduced rotation length with lower selection ratios making establishment and tending cheaper;
2) better quality of products (logs, wood density etc.) arising from improved tree form, disease resistance and better wood quality;
3) increased profit margins as a result of increased volume production (20 to 30 % -Shelbourne 1986), low risk due to improved disease resistance and high quality lumber from improved tree form; and
4) breeding for end-user characteristics of economic value so as to increase profit margins even further.

2.3 NON-CROP VEGETATION MANAGEMENT

2.3.1 Introduction

2.3.1.1 Weeds and non-crop vegetation

The term "weeds" has been (re)defined by various researchers differently, but perhaps the shortest definition is that weeds are any plants "growing out of place". In agricultural and forestry contexts, the plants growing out of place would be those that were not sown and therefore are not part of the main crop to be harvested. A comprehensive definition of weeds is that by Stearn (1956);

> *"taken as a whole, weeds are not so much a botanical as a human psychological category within the plant kingdom; for a weed is simply a plant, which in a particular place at a particular time, arouses human dislike; and attempts are made at its eradication and control, and because it competes with more desirable plants, and because it serves as a host to their pests and diseases, or is unpalatable or dangerous to domestic beasts".*

The name weed is therefore, a subjective term describing the unwantedness or undesirability both in space and time of less appealing plants. Desirable or wanted crop trees in forestry monocultures are defined as the main species to which all management efforts and resources are aimed. In a forestry context any unwanted plants growing together with the desirable crop trees are termed weeds (Auld *et al.* 1987, Walstad and Kuch 1987). In recent times weeds in plantations have become known as non-crop vegetation, a term encompassing all species (both wanted and unwanted) growing in the vicinity of desirable crop plants. Non-crop vegetation can therefore be defined as plants of the same, or of a different species to the crop trees; their presence on the site may be beneficial, for example, N_2-fixing species on poor soils (West and Dean 1992) or detrimental to the healthy vigorous growth of the main crop trees (Walstad and Kuch 1987, Kirongo 1996). The term "non-crop" recognises occasional beneficial effects conferred on other plants.

2.3.1.2 Some Important biological and ecological attributes of weeds

Weeds have been known for millennia to be very aggressive plants; easily adapting and out-competing their neighbours and showing high resilience to adverse environmental conditions (Auld *et al.* 1987, Gjerstad and Barber 1987, Holt 1988). As King (1966) wrote;

> *"weeds as a class probably represent the most successful plant forms which have evolved simultaneously with the destruction or disruption by man of the indigenous vegetation and its habitats".*

Similar views are shared by many researchers as well (e.g. MacFadyen 1998), who noted that most present-day weeds were formerly introduced as ornamentals or forage species for pet animals but have multiplied to unmanageable levels.

Weeds have rapid growth with prolific seeding or vegetative reproduction habits (Holt 1988), which can lead to successful colonization of bare sites or re-invasion in sites where eradication is sought (Gjerstad and Barber 1987). Some weeds have specialized seeds called diaspores with high dispersal rates. Physical characteristics of the diaspores, for example lightness, hooks to readily attach to dispersal agents (animals, birds) and hard seed coat resistant to digestion in animal/birds' tracts favour ease and wide dispersal range (Auld *et al.* 1987). Some species produce allellopathic chemicals which inhibit the healthy growth of neighbours (Berkowitz 1988) or protect against intense browsing by herbivores (Auld *et al.* 1987).

2.3.1.3 Weed control and non-crop vegetation management

Weed control was a term used to imply the complete removal (total control or no control) from the site of the unwanted vegetation (Walstad and Kuch 1987). In contrast, non-crop vegetation management is a more accommodating practice requiring an understanding of the basic biological and ecological processes of the non-crop vegetation. The weeds are controlled only to levels and for a duration that is needed to optimise crop growth and meet management objectives. Physical, mechanical, chemical or biological approaches singly or in an integrated fashion, are employed to achieve cost-effective and environmentally friendly control levels of the

less desirable species (Walstad and Kuch 1987, Fryer 1987). The emphasis is, therefore not on complete elimination of the weeds but rather on minimizing the deleterious effects to levels which do not cause significant growth or harvest losses of the crop plants.

Non-crop vegetation is economically important in forestry and agricultural systems and has been quoted as the major cause of economic losses and environmental damage (MacFadyen 1998). In young plantations before canopy closure, managers are mostly concerned with inter-specific competition (between different species as opposed to intra-specific competition, which occurs between plants of the same species as may occur after canopy closure) for limited resources especially water, nutrients and light. Management interventions aim to release the crops at reasonable costs (Evans 1992, Chapman and Allan 1978, Radosevich and Oysteryoung 1987, Zabkiewicz and Richardson 1990).

2.3.1.4 Interference and competition

In plants, interference can be defined as the positive or negative interaction between two plants sharing the same growing environment (Radosevich and Oysteryoung 1987). Positive interference occurs where both plants benefit from the association, for example symbiotic N_2-fixation. In some instances, one plant benefits from the association while the other loses e.g. parasitism or predation. Competition is a special case of interference where both plants do not benefit from their association.

Competition in forestry is defined as the sum of all the negative interference effects experienced by an individual tree due to the proximity of another (Radosevich and Oysteryoung 1987). Competition can be between plants of the same species (intra-specific) or plants of different species (inter-specific). Inter-specific competition is the most important form of competition in young intensively managed monocultures (Walstad and Kuch 1987, Evans 1992, Richardson 1993). Previous studies have shown that weeds usually need to be controlled promptly to ensure successful plantation establishment (Squire 1977, Nambiar and Zed 1980, Balneaves 1981, Evans 1992, Boyall 1983, Sands and Nambiar 1984, Will 1985, Brand 1986, Nambiar and Sands 1993, Mason 1992, Balneaves and Clinton 1992, Comeau *et al.*

1993, Perry *et al.* 1993, Wagner and Radosevich 1991a, Richardson 1993, Markin and Gardner 1993, Kirongo 1996, Richardson *et al.* 1996b, Mason and Kirongo 1999).

2.3.2 Importance of non-crop vegetation management

Non-crop vegetation has both advantages and disadvantages, however. Advantages include protecting soil against erosion (Comeau *et al.* 1993) and forage for livestock and wildlife (West and Dean 1990). Nitrogen fixing species ameliorate poor sites, hence the move to oversowing bare sites with easy-to-manage N_2-fixing species (West and Dean 1992, Richardson 1993, Richardson *et al.* 1996a). In pasture sites in New Zealand White clover (*Trifolium repens*), which is considered a 'weed' in this study is worth billions of dollars to the New Zealand pastoral and apiary industries (Roy *et al.* 1998). Some non-crop vegetation can offer mulching effects (Walstad *et al.* 1987) or buffer young crops against damaging winds (Kirongo 1996). Non-crop vegetation can also increase total productivity of some agroforestry systems (Auld *et al.* 1987, Liebman 1988, Van Rossen and West 1993). Weeds are also useful as indicators of site quality (Parham and Healy 1976). Meanwhile, Menzies *et al.* (1981) and Menzies and Chavasse (1982) cite the removal of weeds in high altitude sites to decrease surface albedo and as a result reduce the likelihood of out-of-season frosts which can kill the tender growing shoots of young radiata pine.

Non-crop vegetation is economically important in forestry and agricultural systems due to its less desirable properties, in particular competition for limited site resources, thus warranting its control (Smethurst and Nambiar 1989, Wagner and Radosevich 1991a,b, Evans 1992, Richardson 1993, Lowery *et al.* 1993, DeLong 1991, Nambiar and Sands 1993, Richardson *et al.* 1996a,b, Zutter *et al.* 1986, Zedaker *et al.* 1993, Willoughby 1999, Zutter *et al.* 1999a,b); an age-old problem, as noted by Shakespeare (The tragedy of King Richard II, Act III, scene IV, line 37-39):

"I will go root away
The noisome weeds, which without profit suck
The soil's fertility from wholesome flowers."

In some New Zealand sites gorse and broom compete aggressively for boron and phosphorous (Balneaves 1981). Further, Balneaves (1981) reports some weeds (for example gorse) to persist as understory vegetation and continue to compete aggressively long after the establishment phase. Unwanted species can also compete for water and other nutrients (Nambiar and Zed 1980, Smethurst and Nambiar 1989, Nambiar and Sands 1993, Sands and Nambiar 1984, Richardson 1993) especially in dry sites or light (DeLong 1991, Comeau *et al.* 1993, Cannell and Grace 1993, Richardson *et al.* 1996b, 1999). Smethurst and Nambiar (1989) reported increased foliar nitrogen in seedlings which had received weed control. Zutter *et al.* (1999a) found non-crop vegetation control to increase loblolly pine fascicle mass. However, they got mixed trends regarding nutrients depending on site characteristics and weeding treatment. In another related study Zutter *et al.* (1999b) reported competition from broom sedge to reduce fine root growth and density of loblolly pine and sweet gum in the top 15 cm of soil. They further reported interspecific competition effects on fine root growth to be similar to those observed for above ground structures. In both studies most competition effects occurred in the first two growing seasons underpinning the importance of non-crop vegetation control during this period.

Non-crop vegetation can "smother" (physical contact causing abrasion) crops and reduce volume and value (Balneaves 1981, Balneaves and Clinton 1992, Boyall 1983, Maclaren 1993, Richardson 1993). Excessive and difficult-to-control (e.g. thorny weeds such as gorse) non-crop vegetation can interfere with and increase operational costs of routine management procedures, for example thinning and pruning (Balneaves 1981, Balneaves and Zabkiewcz 1981, Markin and Gardner 1993). Meanwhile, highly inflammable species increase the risk of fires (Balneaves 1981). Squire (1977) and Will (1985) cite fertilization in the presence of weeds to be ineffective and of little benefit to the crop trees. MacDonald *et al.* (1999) observed significant genetic growth differences between improved and "nursery-run" stock

only after weed control. Thus, managers need to appreciate that the gains from using improved genotypes may be compromised if weeding is not done in a timely fashion.

Therefore, the timely removal of excessive non-crop vegetation is an important and sometimes a mandatory silvicultural operation in the successful regeneration of most commercial plantations. The undesirable effects of non-crop vegetation are two-fold:

1) the potential to interfere with the hypothesized stand development if the "weeds" are not controlled sufficiently and in a timely fashion (Tappeiner and Wagner 1987); and
2) the fact that "weeds" may also lower crop quality by affecting stem form or reducing final yields (Balneaves 1981), especially in agriculture (Boyall 1983) resulting in reduced profit margins.

Some general considerations for controlling weeds include (Walstad and Kuch 1987):

1) the economic efficiency of the exercise at the time;
2) the growth losses which will be incurred if treatment is deferred or postponed; and
3) the ability of the desired plants to grow vigorously once they have been released from stress.

Moreover, managers should bear in mind that in dry sites weeds lower not only current rates of growth but also reduce future levels of potentially attainable growth by reducing current leaf areas (Kirongo *et al.* in prep.).

2.3.3 Common methods of non-crop vegetation management in plantations

Competition occurs whenever resources are limiting and trees with similar resource needs (nutrients, light, moisture) and/or similar growth habits share the same micro-environment or niche (Radosevich and Oysteryoung 1987). In young plantations, managers are more concerned about inter-specific competition. However, intra-

specific competition is also important later in the rotation necessitating thinning and/or pruning.

In plantations the planted trees represent large investments. It is for this reason that all management interventions (weeding, fertilization, irrigation), (Evans 1992, Chapman and Allan 1978) are normally aimed to favour crop trees. Alleviation of negative interference is very important. Competitors, tend to limit the growth potential of the desired crop trees by pre-empting resources (water, light, nutrients), (Radosevich and Oysteryoung 1987, Berkowitz 1988). Consequently, managers normally reduce or eliminate competition altogether by removing all competitors and potential competitors to ear-marked crop trees (Evans 1992, Chapman and Allan 1978, Cannell and Grace 1993, Radosevich and Oysteryoung 1987). This is called weed control and is part of the plantation tending program of any commercial forestry venture.

The decision to control or not to control may be influenced by the following three factors (Walstad and Kuch 1987, Evans 1992);

1) the importance of non-crop vegetation in altering the envisaged plant growth,
2) knowledge of the time(s) when the interference effects are most detrimental,
3) the availability of resources and control methods which are acceptable environmentally, social-culturally as well as politically (for example some legislation may not allow use of certain chemicals) and the trade-offs involved.

Meanwhile the knowledge of the growth form and habits of the main weed species is an important prerequisite to designing efficient and effective control programs. The most common control methods include cultural, chemical, Biological and Integrated approaches (Evans 1992, Richardson 1993, MacFadyen 1998).

2.3.3.1 Cultural or physical means

Cultural methods of weed control include manual and mechanical methods (Auld *et al.* 1987, Evans 1992, Richardson 1993). Some harvesting and site preparation techniques (e.g. use of fire) can also result in weed reduction (Auld *et al.* 1987, Mason 1992, Richardson 1993, Maclaren 1993). Chemicals used for site preparation may offer some long-term weed control, as well (Preest 1985). Manual methods are labour intensive and are the main weed control methods in many tropical forest plantations (Chapman and Allan 1978, Evans 1992, Lowery *et al.* 1993). However, some notorious weeds are not easily controlled by these methods e.g. rhizomatous weeds. What's more the efficacy of most manual methods is short-lived calling for more frequent treatments (Willoughby 1999) compared to chemical methods, for example. Meanwhile the use of fire may break the dormancy (Evans 1992) of hard-to-control species e.g. *Acacia* species.

2.3.3.2 Use of chemicals/herbicides

Chemical control methods are the main weed control methods used in New Zealand and Australia (Richardson 1993). Systemic compounds are used to kill the weeds with very good success rates. Some compounds are radiata pine friendly with broad selectivity and low labour requirements (Richardson 1993, Richardson *et al.* 1996a,b). However, responsible use of chemicals is needed to minimise chemical drift, or damage to non-target tree species and animals (Zabkiewicz and Richardson 1990). Excessive long-term use of some chemicals may favour the domination by certain weeds (Nambiar and Zed 1980, Walstad *et al.* 1987, Auld *et al.* 1987). Long-term frequent use of herbicides may not be a real concern in forestry as on average any site would receive herbicide applications once or twice in a 25-30-year rotation period. However, in nursery situation excessive chemical use may be of concern.

2.3.3.3 Biological control methods

Biological control is defined as the use of living organisms to control other organisms (Markin and Gardner 1993). Current Bio-control methods include the use of predators, herbivores, parasites and pathogens to control insect pests, diseases and unwanted weeds (Lawton 1990, Markin and Gardner 1993, MacFadyen 1998). Bio-control methods have been used successfully where other methods have not

succeeded or where site and/or environmental conditions make the use of chemicals unreasonable (MacDonald and Fiddler 1993, MacFadyen 1998, Pitt *et al.* 1999). Currently there are numerous bio-control programs in New Zealand, Australia, South Africa, the U.K., U. S. A. and Hawaii (Sutherland and Hill 1990, Radosevich *et al.* 1990, Markin and Gardner 1993, Wagner 1993, MacFadyen 1998, Pitt *et al.* 1999, Harper *et al.* 1999, Willoughby 1999).

Three approaches of agent release are commonly used in Bio-control. These are; 1) inundation - where the disease (mycoherbicide) or insect predators (in sterile form) are used to engulf and overwhelm the target weed species, 2) innoculation - where the control agent is released into the target population and 3) augmentation - where the control agent is synergistically assisted to perform better and faster (Hill and Gourlay 1990).

In New Zealand success has been reported for the control of some weeds using grazing animals (Dale and Todd 1988, West and Dean 1990, Radcliffe 1990), insects (Markin and Gardner 1993, Jessep 1990, Harman and Syrett 1990, Taylor 1990, Hill and Gourlay 1990, Kay and Smale 1990) and fungi or mycoherbicides (McElwee *et al.* 1990, Johnston 1990). Elsewhere, Harper *et al.* (1999) reported the use of the fungus *Chondrostereum purpureum* (Pers. ex Fr.) Pouzar to be as effective as chemicals in controlling Sitka alder and aspen at one site in western Canada. However, Pitt *et al.* (1999) reported chemicals to be better than *C. purpureum* in controlling speckled alder, red maple and aspen in eastern Canada. Moreover, speckled alder was better controlled than the other two species in the study by Pitt *et al.* (1999). What's more one of the fungus isolates showed higher levels of virulence (Harper *et al.* 1999). These results emphasize the importance of species, site and environmental factors in determining control success.

Bio-control methods are still treated with mixed feelings by some researchers and the general public, however. For example, the introduction of foreign insects is not a good option where the weeds are similar to some native plant species or where the weeds have other tangible benefits e.g. grazing or conservation values. Other concerns include for example, the possibility of attacks to non-targeted species,

inability of the control organisms to discriminate non-target species and the potential to turn into agricultural pests (e.g. Markin and Gardner 1993, MacFadyen 1998).

This notwithstanding, MacFadyen (1998) argues that the wholesale and sometimes unwarranted antagonism towards bio-control measures is not helpful, citing numerous cases of successful bio-control programs. MacFadyen (1998) further states that very little evidence exists in the literature of introduced pathogens which turned into pests, emphasising that those that did were already known to be potential pests even before introduction. Therefore, while it is crucial that necessary checks and balances be put in place before any foreign organisms are released into the new environment, the amendment of some rigid laws is critical for sound bio-control research (MacFadyen 1998).

2.3.3.4 Integrated control approaches

Integrated approaches combine all the above three mentioned methods together to ensure the successful control of difficult-to-control species or those in fragile ecosystems which may not be fully controlled by a single method (Auld *et al.* 1987, Wagner 1993, MacFadyen 1998). For example, Pitt *et al.* (1999) and Harper *et al.* (1999) reported increased mortality of woody weeds by the fungus *C. purpureum* if innoculation was done on stumps as opposed to uncut stems.

2.3.4 Challenges in modelling interspecific competition

Many authors have reported the use of qualitative variables to be very effective in competition models than quantitative variables. Qualitative variables are quick to measure and interpret (Commeau *et al.* 1993). Simple indices based on percent cover, height (Commeau *et al.* 1993) and distances to neighbours are very effective in determining competition severity (Wagner and Radosevich 1991a). Richardson (1993) reported qualitative methods of assessing the need for vegetation control to be the predominant methods used by most forest managers in Australia and New Zealand. The major draw-back of qualitative measures are their subjectivity.

Managers desire to have reliable quantitative decision tools to enable them to make unambiguous decisions on how, when and what methods and trade-offs are involved in controlling non-crop vegetation (Walstad and Kuch 1987). Competition is highly dynamic, and quantitative models, which are more superior in their predictive power than qualitative or subjective models, are needed (Brand 1986, Fredricksen *et al.* 1993, Cannell and Grace 1993, Wagner and Radosevich 1991a, Wagner and Radosevich 1998, Richardson *et al.* 1993, 1999, Ter-mikaelian *et al.* 1999). Most quantitative models have included some qualitative measures, especially of weed abundance, however (e.g. Morris and Forslund 1991, Burton 1993, Wagner *et al.* 1989, Kirongo 1996, Richardson *et al.* 1993, 1996b, Wagner and Radosevich 1991a). Aerial photos have been used successfully to estimate cover (Pitt and Glover 1993, 96) while there is increased use of PAR measures in shade indices (Richardson *et al.* 1999, Ter-mikaelian *et al.* 1999) for woody non-crop vegetation.

The use of PAR as a surrogate for percent cover has resulted in mixed outcomes, however. For example, Ter-mikaelian *et al.* (1999) found no apparent advantage of PAR over percent cover assessment by qualified assessors, nor one time PAR measures over an average of several measures in the season. They further stated that the need for qualified technical staff plus operational difficulties (sensor location, calibration and sensitive nature of the readings) made models using PAR measures difficult to adopt by some managers.

2.3.4.1 Modelling competition effects in young stands

Models of interspecific competition effects involve many non-crop species with diverse physiological and morphological characteristics. Most competition models are empirical and static in nature (Burton 1993), being based on periodic or even one time data and may be unreliable for use in different sites and/or species. Exceptions exist, for example, the basal area prediction model for loblolly pine growing with broad-leaved weeds by Burkhart and Sprinz (1984). Effective models should identify short- and long-term growth reduction arising from continued co-existence between "weeds" and the desired crop trees on the site. Useful models should also be able to rank and prioritize stand release operational needs and as a result facilitate efficient use of available resources.

Study approaches should therefore aim to improve present understanding levels and characterise the physiological responses to resource limitation in the micro-environment (Radosevich and Oysteryoung 1987, Nambiar and Sands 1993).

2.3.4.2 The generalized form of competition models

Most competition models are of the general form:

$$CI = f(a_i, dist_i, wht_i, H_{tr}) \qquad (2.1)$$

Where;

CI = measure of competition intensity,

a_i = measure of non-crop vegetation abundance (size, volume, weight),

$dist_i$ = distance from target crop tree or proximity,

wht_i = height of competitor plant and

H_{tr} = crop tree height.

Most models incorporate neighbourhood measures, weed crown dimensions, root abundance and leaf areas. Common model types are neighbourhood models (Wagner and Radosevich 1991a, Wagner and Radosevich 1998, Burton 1993).

Neighbourhood models use the degree of neighbourliness to characterise competition for resources (e.g. Wagner and Radosevich 1991a, Wagner and Radosevich 1998, Kirongo 1996, Richardson *et al.* 1999). Competition indices (CIs), which are often used in neighbourhood models, show the extent of resource sharing or use by neighbours (Burton 1993). CIs can be used to identify critical periods for non-crop vegetation control needs (Wagner *et al.* 1999) as well as to estimate economic thresholds for vegetation control needs. As such they have great potential as decision tools in young plantations (Cousens 1987, DeLong 1991, Wagner *et al.* 1989, 1999). Where competition is mainly for light, the use of shade-indices is very effective (Burton 1993, Cannell and Grace 1993, Richardson *et al.* 1999). Some researchers have used PAR measures successfully to represent competition from overtopping vegetation (e.g. Ter-mikaelian *et al.* 1999, Richardson *et al.* 1999). Richardson *et al.* (1999) derived CIs from some measures of light interception by buddleia (*Buddleja davidii* Frachet) and broom (*Cytisus scoparius* L.) in 0-3-year old radiata pine. They

found that at a particular CIs level, the CIs effects were independent of weed species and age (Goldberg 1996). For more information on competition models, Kirongo (1996) is a useful reference guide.

2.3.5 Experience from previous studies: The Rolleston study

Kirongo (1996) used a neighbourhood approach to study the competitive effects of herbaceous and woody (mainly *Acacia* spp.) weeds on the growth of young plantation-grown radiata pine in Rolleston Canterbury, New Zealand. During the Rolleston study it was observed that some trees which were growing in weed-free status exhibited low growth. This phenomenon was called the "*rich-kid*" effect (Wagner *et al.* 1989). The phenomenon had also been observed in similar studies, for example Wagner *et al.* (1989). It was also evident that the repressive effects of different weed species were strongly influenced by seasonal weather patterns. What's more, competition for light was largely a function of growth form with woody species having different effects on the crop from those of herbaceous species.

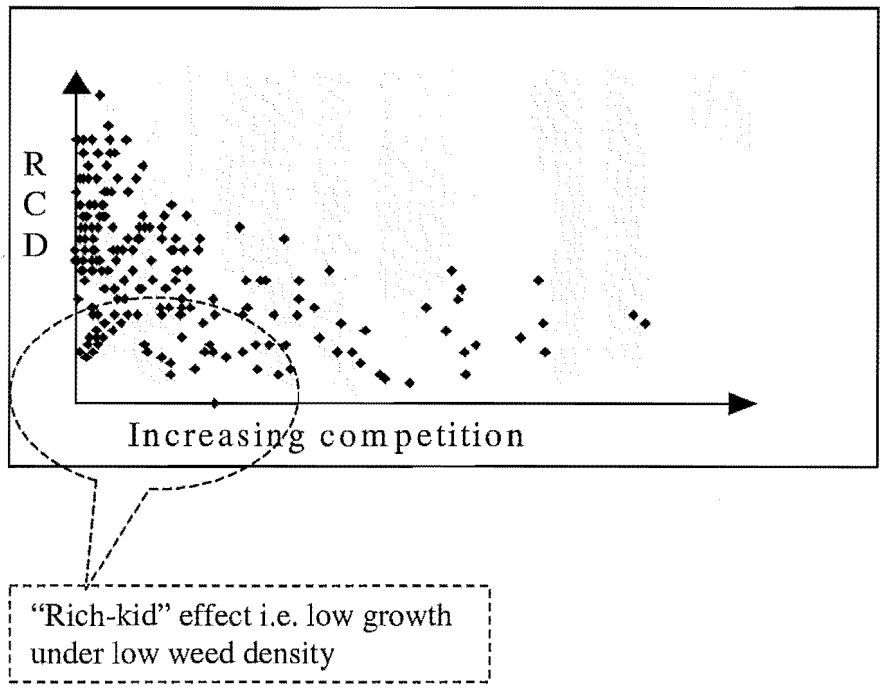

Figure 2.2: The generalized relationship between individual radiata pine root collar diameter (RCD) growth and increasing weed density (After Kirongo 1996, p. 99).

Important factors thought to influence this relationship are itemised below.

1) Poor competition measures due to subjectivity in determining percent weed occupancy - although subjective measures are often better than quantitative measures (e.g. Wagner and Radosevich 1991a).
2) Uneven vegetation cover from one tree to the other – it is crucial to ensure that designs used in weed research minimise variation in weed occupancy between trees in the same treatment (Kirongo 1996), as CIs are often calculated on an individual tree basis.
3) Confounding effects of tree genotype and competition intensity – responses of different genotypes to variation in competition intensity need to be quantified (Kirongo 1996).
4) Micro-site variation, differences in handling and planting quality (Mason in prep.).

Mason and Kirongo (1999) did not find evidence for a "rich-kid" effect in a 2 year genotype-by-weed competition study at Dunsandel. However, a year later Kirongo *et*

al. (in prep.) found a significant genotype-by-weeding interaction for height growth in the same experiment, but still no rich-kid effect. Mason and Kirongo (1999) discussed the possible reasons for the rich-kid effect observed in previous studies. They suggested that use of 3-D graphs and statistical tests on coefficients of variation of CIs classes would be more informative. Meanwhile, other factors which are usually not included in weeding studies may contribute significantly to the observed variation in tree growth between treatments for example, animal browsing and defoliation or changes in seasonal weather patterns (Wagner and Radosevich 1991b).

2.3.6 Summary

Weeds form an important economic component in forestry and agroforestry systems. In the developing world 60% of total maintenance labour in forestry systems is devoted to hand weeding (Webb and Conroy 1995). Weed control consumes 47% of the world's agrochemicals. Given that uncontrolled weeds can affect the healthy development of tree crops, it is important therefore to have reliable ways to assess and control inter-specific competition in plantations. A well designed Decision Support System (DSS) should therefore have initial growth models with the capability to predict accurately under conditions of variable weed densities.

Competition models are peculiar in that many species with diverse resource needs and growth forms share the same micro-environments. Studies of inter-specific competition may need seasonal data especially during the main growing season when resource deficits are severe (Kirongo 1996, Madgwick 1994). For example, the effects of moisture stress may be exacerbated by the presence of weeds during the summer months when moisture levels are lowest.

In modelling competition, sensitive models may have to allow for specific species related resource needs. That way it may be possible to predict and manage the negative effects of useful weed species. For example the presence of nitrogen fixers may offer benefits even though they may compete for available water resources. This is in contrast to weed species, which have no nitrogen fixing ability. The cost of

having such species in terms of competition for moisture need to be evaluated and compared to the benefits they provide. Meanwhile, some weed species (e.g. rye grass) can increase CO_2 levels in the soil, which affects young radiata pine root growth (Zou *et al.* 2000). Thus when oversowing, it may be important to know the species' root respiration habits as species with heavy root respiration can lead to elevated CO_2 levels in the soil with dire consequences to the radiata pine (Sands *et al.* 2000). Moreover, reduced soil moisture levels can affect other soil physical properties e.g. aeration and soil strength, which in turn may reduce radiata pine root growth (Sands *et al.* 2000).

2.4 PLANT GROWTH FORM AND STRUCTURE

Plant structure is the product of past growth activities and the environment. Present structure and functioning determines the rate of growth and other biochemical activities. In mature plants, most carbon is in the form of structural material (e.g. for support) and is not directly involved in C-fixation. This is not the case with juvenile plants growing actively, where leaf biomass forms a substantial fraction of the total plant dry weight.

Progress in studies of plant structure and allocation have not kept pace with other fields mainly because of the labour-intensive and expensive nature of gathering biomass data (Snowdon 1985, Landsberg 1986, Madgwick 1994) on the one hand, and the use of intrusive methods that kill the plants, added to lack of conformity of research laboratory results when applied to open-grown trees, on the other. In particular, the lack of quantitative data on environmental and silvicultural effects to enable development of explicit mechanistic models has been a disincentive for their easy of adoption as management tools (Beets and Whitehead 1996). The use of easily measurable variables for example stem height and diameter as predictor variables of allocation patterns has major flaws as well. The most significant draw back is the fact that stem growth (height and diameter) is not only insensitive to seasonal variation in resource pools (Pook 1984), but also dependent on the dynamics of foliage and roots

turn-over which vary significantly with season, the prevailing environment and site (Waring and Running 1998). Therefore, their use could lead to bias.

Plant growth is dependent on the processes of photosynthesis and respiration. Photosynthesis harnesses sunlight energy and CO_2 into carbohydrates, while respiration oxidizes stored assimilates to release energy for various plant metabolic processes. Therefore it is only proper that before discussing allocation to various plant parts, a brief mention be made regarding the processes of photosynthesis and respiration.

2.4.1 Photosynthesis and Respiration

2.4.1.1 Photosynthesis

Photosynthesis is defined as the biochemical processes in leaves of green plants through which energy from the sun, absorbed by chlorophyll, is used to split water molecules into hydrogen and oxygen which are combined with carbon dioxide to produce a carbohydrate moiet (Charles-Edwards *et al.* 1986, Waring and Running 1998). The interim products or moiety are used to make more complex compounds. Mathematically this is represented as:

$$n(CO_2) + n(H_2O) \xrightarrow{light} (CH_2O)n + n(O_2) \qquad (2.2)$$

where;

CO_2 = carbon dioxide,

H_2O = water,

CH_2O = carbohydrates,

O_2 = oxygen and

n = constant for the number of molecules.

Factors affecting the rate of photosynthesis include CO_2 concentration, irradiance, temperature and moisture. The photosynthetic process has two main phases; light- and dark-reaction. The light reaction phase is used to generate adenosine triphosphate (ATP) and a reduced form of nicotinamide dinucleotide phosphate (NADPH) and is dependent on irradiance levels and chlorophyll content. The dark

reaction phase is used to reduce CO_2 into C3 or C4 carbon compounds (Charles-Edwards *et al.* 1986). The dark reaction phase of photosynthesis is dependent on CO_2 and temperature, as well as N_2 levels for the production of the necessary enzymes used in the process (Waring and Running 1998).

The diffusion rate of CO_2 into the reaction sites can slow down the photosynthetic process significantly. CO_2 diffusion is governed by CO_2 partial pressure and stomatal conductance. Meanwhile water, which is needed for other biochemical processes of plant growth, is also crucial for stomatal conductance as well. Water stressed trees close their stomata and cut off CO_2 diffusion into the leaves. Prolonged moisture stress can lead to enzyme and chlorophyll breakdown making the tree unable to function properly (Waring and Running 1998).

Trees can carry out photosynthesis at optimal rates in temperatures between 10-35 ^{o}C depending on the geographic zone. However most biochemical reactions slow down at very low temperatures or above 40 ^{o}C and completely shut off above 50 ^{o}C. Extremes of temperatures are detrimental to proper functioning of the plant, can denature enzymes and significantly affect photosynthesis (Perkins and Adams 1995).

Above the light compensation point, CO_2 and the enzyme ribulose bisphosphate (RuBP) limit photosynthesis. Light compensation point occurs when CO_2 from respiration is balanced by use from photosynthesis and net assimilation = 0. Maximum levels of leaf photosynthesis generally decrease linearly with canopy depth and leaf age. Meanwhile care should be taken when relating leaf nitrogen with photosynthetic capacity of leaves as total leaf nitrogen includes nitrogen other than that used in the photosynthesis process (Waring and Running 1998).

2.4.1.2 Light use efficiency

Photosynthesis uses a range of light wave lengths called photosynthetically active radiation (PAR), (Grace *et al.* 1987a, Charles-Edwards *et al.* 1986, Waring and Running 1998). The PAR range is between 400 - 700 nm (0.4 - 0.7 μm). Light use efficiency (Є) is defined as the ratio of dry matter turn-over to the amount of PAR absorbed by the plant (Charles-Edwards *et al.* 1986). It shows the efficiency with

which a plant uses intercepted PAR to produce dry matter. Mathematically, light use efficiency can be expressed as,

$$\epsilon = \frac{\Delta W}{j} \qquad (2.3)$$

where;

ϵ = light use efficiency, ΔW is dry weight change and J = intercepted PAR. Charles-Edwards *et al.* (1986) reported typical ϵ values to be 2.5 μg (dry matter) J^{-1}.

The daily amount of intercepted PAR (J) by a tree canopy depends on two factors; 1) the integral of incident energy (S) and 2) the proportion of light absorbed by the canopy (Q) during the day. For 'closed canopies' (i.e. those in which light flux density is the same in all directions), the amount of PAR absorbed can be expressed as:

$$Q = 1 - \exp(-kL) \qquad (2.4)$$

where;

k = canopy light extinction coefficient and L = LA of the canopy.

Canopy light extinction coefficient (k) shows the light attenuation patterns as it travels through the canopy. Crown architecture and leaf mosaics (i.e. inclination and orientation of individual foliage) plus leaf area density (i.e. LA in a volume of the crown) will influence k through their effects on light attenuation patterns as it travels through the canopy. Canopy light extinction coefficient is the main determinant of light use efficiency. Meanwhile, individual leaf efficiencies (quantum yield) and the CO_2 conversion efficiency into dry matter have significant effects on plant light use efficiency (Charles-Edwards *et al.* 1986).

The photosynthetic capacity of leaves in different canopy positions differs (Grace *et al.* 1987a,b, Wang and Jarvis 1990) and leaves deeper in the canopy have lower capacities than their counter parts above the canopy (Charles-Edwards *et al.* 1986).

2.4.1.3 Respiration and dark respiration

Plants need energy to run their metabolic activities. The break down of stored carbohydrates to produce energy is called respiration. Dark respiration is a special

form of respiration when the interim products of photosynthesis rather than stored carbohydrates are broken down to produce CO_2 (Charles-Edwards *et al.* 1986, Waring and Running 1998).

Respiration is useful to produce energy for the upkeep of the plant (maintenance respiration) as well as for the formation of new structural material (constructive respiration). Of the two, maintenance respiration is a function of plant size. It is highly influenced by the rate of protein turn-over and not the content (Charles-Edwards *et al.* 1986).

2.4.2 Plant growth and allocation

Sound mechanistic models of tree growth should have accurate sub-models of dry matter partitioning to different tree components, especially roots, stem, branches and foliage. The models should also cater for changes in allocation patterns brought about by micro-site changes and silvicultural inputs (Baker *et al.* 1984, Snowdon and Benson 1992) as well as age differences (Landsberg 1986, Rook *et al.* 1987, Beets and Whitehead 1996). Moreover, genotype affects carbon partitioning significantly (Snowdon 1985, Snowdon and Waring 1985, Madgwick 1983b, Theodorou *et al.* 1991) and may result in different clones showing different degrees with which they withstand environmental stresses (Waring and Running 1998). The amount of photosynthate held in leaves and roots, for example, significantly influences water and nutrient dynamics of the plant as well as radiation interception, photosynthesis, transpiration and ultimately growth.

2.4.2.1 Allocation to stem and branches

Where water and nutrients are not limiting, allocation of above ground biomass has been reported to increase in the stem with increasing tree age (Madgwick 1994). Allocation to branches and stem bark remains relatively constant. Beets and Pollock (1987) reported increased annual partitioning to stems with increasing age (35% to 60% between ages 2 to 12), while partitioning to branches remained unchanged. In other related studies, branch biomass increased to a maximum at age 30 years then

tapered off, while stocking did not appear to have profound effects (Madgwick 1981, 1994). Genetics influenced allocation to stem and branches (Snowdon 1985, Snowdon and Waring 1985) through its effects on branching habits and overall branch size (Madgwick 1994).

Allocation to stems can be approximated by the function;

$$\ln(Ws) = -3.56 + 1.10 * \ln(h) + 0.62 * \ln(ba + 1) + 0.36 * \ln(age) + 0.28 * \ln(sph) \quad (2.5)$$

where;

ln = natural logarithm, Ws = stem weight t/ha, h = stand height, ba = basal area m^2, age = stand age in years and sph = stocking per hectare (Jackson and Chittenden 1981).

A number of other functions have been used to estimate allocation to stem and branches. For example, Madgwick (1983a) used a pooled data set from New Zealand, Australia and South Africa and fitted a function for total stem biomass;

$$\ln(W) = -4.892 + 1.028 * \log((d + 1.9)^2)h \quad (2.6)$$

where; W = stem biomass, d = diameter at breast height, h = tree height.

Most of the functions used differed in their parameter estimates due to the effects of genetics, silvicultural treatments and age (e.g. Baker *et al.* 1984). Therefore, it is good practice to check the reliability of generalized equations by carrying out a pilot study for the site, species, age, genotype and silvicultural treatments (Baker *et al.* 1984, Snowdon 1985, Madgwick 1994).

It is also important to note that most of the functions in the literature refer to trees growing in stress free environments or trees which have closed canopy. There is a paucity of information on allocation patterns of trees which are 3 years old, or less and growing under variable microenvironments and integrating genotypes.

The proportion of biomass allocated to branch wood and stem wood is highly influenced by genetics (Snowdon 1985, Snowdon and Waring 1985). This has significant effects on management because clones with high proportional allocation

to branches incur heavy branching. This may reduce their stem wood and increase operational costs (e.g. pruning). It is also possible that such clones may carry a high risk of wind damage in areas which are wind-prone such as Canterbury.

Madgwick (1983a) found the function,

$$\ln(W) = -5.336 + 2.835 * \log(d_c) \qquad (2.7)$$

to fairly describe allocation to live branches of a pooled data set. Total branch biomass (live and dead) was described by,

$$\ln(W) = -4.189 + 2.448 * \log(d_c) \qquad (2.8)$$

Meanwhile, Snowdon and Benson (1992) found the function,

$$\ln(W) = a + b * \ln(d) + c * \ln(h) \qquad (2.9)$$

to best fit their stem wood and bark data, while Ek (1979) used the function;

$$W = b_1 * d^{b_2} * (h - h_b)^{b_3} * (h/d)^{b_4} \qquad (2.10)$$

In all cases d = dbh, dc = diameter at the base of live crown, h = tree height, hb = height to branch base and a, b, c were constants. Changes in taper due to site, management inputs or genotype were presented by the use of h and d (Snowdon and Benson 1992) or h/d (Snowdon 1985, Ek 1979).

2.4.2.2 Allocation to foliage

In a study of above ground dry matter content in a closely spaced (1x1.5 m) 5-10 year-old radiata pine stand, Madgwick (1981) reported that the weight of one-year-old foliage varied very slightly around 7.8 t/ha with increasing tree age. Total tree leaf area index (all surfaces) increased with stand age for above ground production. Foliage weight was variable but normally maximized at about 15-19 t/ha between age 4-8 years (canopy closure) before falling (Beets and Pollock 1987). In the study by Beets and Pollock (1987) partitioning to leaves decreased from 40% at age 2 to 20% by age 12 years. The average partitioning to leaves over the period was 27%.

In another study, Madgwick (1993) found the ratio of branch to foliage in a 5-13 year-old stand to be constant at 0.75. Crown position, tree age and size had insignificant effects on the ratio. He cited crown closure to be the cause of the decline in allocation to crown and foliage compared to stem. In similar studies

elsewhere the ratio varied between 0.68 to 1.03 (Madgwick 1983a, Mead *et al.* 1984, Beets and Pollock 1987, Snowdon and Benson 1992) with significant age, genetics and silviculture effects (e.g. Madgwick 1983b, Baker *et al.* 1984).

Foliage weight variation within the year was a function of the stage of stand development (canopy closure) and the environment (Madgwick 1994) with temporal differences governed by position in the canopy (Raison *et al.* 1992a). Older stands had proportionally less current season foliage (Madgwick (1994).

Madgwick (1994) reported that foliage weight could be estimated from stand basal area by the function:

$$\ln(W_f) = -1.337 + 0.742 * \ln(ba + 1) + 1.478 * \ln(a) - 0.404 * [\ln(a)]^2 \qquad (2.11)$$

where;

W_f = foliage dry weight, ba = basal area, a = age of the stand.

Madgwick (1983b) used the function,

$$\ln(W) = -3.952 + 2.193 * \log(d_c) \qquad (2.12)$$

while Snowdon and Benson (1992) used a quadratic function with dbh as the independent variable.

2.4.2.3 Allocation to roots

Studies of below ground allocation have not kept pace with those of above ground allocation. Below ground allocation can account for up to 50 % of the total tree biomass, especially in water stressed trees (Landsberg pers. comm. - seminar). However, measurement of below ground allocation has its unique problems that can be a deterrent. For example, the intricate dynamics of fine root turn over both in space and time, and in particular, the difficulty of extracting very fine roots undamaged or avoiding contamination with ash or minerals are of major concern. Jackson and Chittenden (1981) went round this problem by using containers or polythene-lined trenches to grow the trees. This ensured that all roots could be recovered from the volume of soil in the containers. They found a high correlation (r = 0.961) between fine root dry weight (roots < 2 mm diameter) and small roots (2 mm - 5 mm). Thus fine roots dry weight could be estimated using fine root dry

weight which is relatively easy to extract. Further, they correlated fine root dry weight to foliage dry weight (r = 0.914). Jackson and Chittenden (1981) expressed total fine root dry weight of 3-8-year old radiata pines growing in water and nutrient stress-free environments as functions of foliage dry weight:

$$Fine\ roots = -121.35 + 0.526 * (foliage\ dry\ weight) \qquad (2.13)$$

Jackson and Chittenden (1981), further described the oven dry weight of roots as a function of diameter at breast height using the function:

$$Roots = \alpha * (dbh)^{\beta} \qquad (2.14)$$

The estimated coefficients for roots > 2 mm diameter were, $\alpha = 5.97$ and $\beta = 2.8068$, while for roots > 5 mm in diameter $\alpha = 6.25$ and $\beta = 2.7382$. Moreover, they found the function;

$$\log(Roots > 5\ mm) = -5.009 + 2.7296 * \log(dbh) \qquad (2.15)$$

to fit well to pooled data from earlier studies.

It is important to note that the use of foliage weight to estimate root weight is not reliable for trees that have closed canopy, because of 1) changes in allometric relationships and 2) trees allocating more to stems and less to foliage after canopy closure. Jackson and Chittenden (1981) pointed out that in the event of foliage diseases the equations may under-estimate root biomass as roots were less likely to be heavily infected compared to foliage.

2.4.2.4 Effects of some management inputs on allocation patterns: thinning, fertilization and irrigation

Alleviating nutrient deficits, for example through fertilization leads to changes in allometry and allocation patterns (e.g. Baker *et al.* 1984, Snowdon 1985, Mead 1990, Snowdon and Benson 1992). Fertilization with nitrogen has been reported to increase foliage mass (Brix 1981, Mead *et al.* 1984, Baker *et al.* 1984, Hunter *et al.* 1987). Increased photosynthate was more an effect of increased foliage than a change in foliage efficiency *per se* (Mead *et al.* 1984), contrary to Brix (1981) who reported increased leaf efficiency in Douglas-fir.

Thinning and fertilization increased allocation to above ground dry matter (Brix 1983). Meanwhile Snowdon and Waring (1985) reported increased coarse root biomass fraction in four-year old radiata pine in Australia following fertilization. Further, fertilization and thinning resulted in increased allocation to crown at the expense of stem. Snowdon and Benson (1992) concurred with these observations, adding that trees in the control had reduced above ground allocation.

In a study integrating effects of canopy closure and alleviation of intra-specific competition (by pruning and thinning) in the absence of water and nutrient stress, Beets and Pollock (1987) found basal area growth rate of *P. radiata* to increase to a maximum (10 m^2/ha/yr) by age 4 years, but to decrease to 3-4 m^2 /ha/yr by age 12. Foliage weight peaked at 19 t/ha by age 6, while leaf area index (L.A.I. all surfaces) reached a maximum at age 6 (L.A.I. = 34); both variable values falling thereafter irrespective of thinning treatment. During the study period annual partitioning rates to leaves and stems decreased, while partitioning to branches remained constant. Stand age was more important in determining allocation patterns than thinning. Further, above ground production for a given leaf area index increased with stand age implying that a shift in allocation from roots to stem was probable rather than a change in production efficiency. This may mean that direct estimates of above ground production from intercepted radiation incurred some bias, unlike those from total production.

2.4.2.5 Allocation and competition

Biomass allocation to various plant organs may vary depending on tree age, species, site and resources competed for. Carefully controlled studies covering a broad range of the "common" management and silvicultural procedures used, species and their genotypes are needed.

Conflicting results have been reported in some allocation studies of trees growing under resource deficits. For example, Newton and Jollife (1993) reported increased allocation to bark and foliage with a **decrease** to stem and branches under increasing competition in 2-year-old *Picea mariana* contrary to Nilsson and Albrektson (1993) who reported **increased** allocation to stem wood under competition. Munson and

Timmer (1990) reported seedlings of *P. mariana* under nutrient stress allocated more to stem and roots. Chang *et al.* (1996) found the removal of understorey competition to increase above ground allocation. They further reported that weeded plots had higher allocation to roots (roots > 1 cm diameter) than the controls. This is reasonable bearing in mind that there is a strong relationship between foliage mass and root weight (Jackson and Chittenden 1981). However, this is in disagreement with other studies which reported water-stressed trees (for example due to weed competition) to allocate proportionally more photosynthate to roots (Madgwick 1994, Landsberg pers. comm. - seminar). The relationships may also not hold across competition gradients and studies tailored specifically to answer these questions are needed.

2.5 MODELLING CANOPY STRUCTURE AND FUNCTION

Tree growth is related to the amount of leaf area and the efficiency with which the foliage converts intercepted useful energy into carbohydrates, as influenced by the foliage spatial and temporal distribution (Grace *et al.* 1987a,b, Hunter *et al.* 1987, Leverenz *et al.* 1982, Beadle *et al.* 1985, Charles-Edwards *et al.* 1986, Wang and Jarvis 1990). The crown shape, morphology and branch architecture influence the leaf mosaics (Wang and Jarvis 1990) and vary greatly between trees. This in turn causes different crown parts to have different leaf area spatial distributions resulting in variation in light penetrability, CO_2 and water vapour levels and hence photosynthesis (Kinerson *et al.* 1974, Landsberg 1986, Leverenz *et al.* 1982, Wang and Jarvis 1990). The efficiency of leaves to convert intercepted useful light energy into carbohydrates decreases with age (Woodman 1971, Watts *et al.* 1976, Xu 2000) and crown depth (Charles-Edwards 1986, Grace *et al.* 1987a,b). Thus the proportion of the various leaf-age classes present in the crown needs to be known, as well as the light attenuation patterns and leaf area density (Landsberg 1986, Grace *et al.* 1987a,b; Xu 2000).

Grace *et al.* (1987a,b) successfully developed models of canopy photosynthesis using intercepted radiation and accounting for differences in crown shape and light use

efficiency of different foliage age classes within crowns, for water and nutrient stress-free radiata pine in the North Island of New Zealand. Xu (2000) developed similar models for 5-year old individual radiata pine tree clones growing in a dry environment in the South Island, New Zealand. The study reported here investigated foliage growth dynamics and factors which influenced needle mortality in juvenile radiata pine clones. Foliage growth and losses are important variables in canopy production models.

2.5.1 Foliage growth dynamics

The amount and growth rate of new foliage is important in determining gross production. In stress-free environments new foliage can attain full size in a short time with maximum leaf areas and hence increased PAR absorption and C-fixation (Rook and Whyte 1976, Beadle *et al.* 1985, Dalla-Tea and Jokella 1991). The physiological state of the foliage is also an important determinant of photosynthate production (Charles-Edwards *et al.* 1986, Menzies *et al.* 1991). Trees with proportionally higher amounts of young foliage are better able to fix more carbon than their counterparts, which may have similar foliage amounts but of older ages. Thus the total amount of foliage, its spatial and temporal distribution as well as its physiological state will all influence carbon fixation and growth.

Needle growth (elongation) in a growing season has been successfully modelled using logistic functions (Kinerson *et al.* 1974, Rook *et al.* 1987, Bandara 1997). However, the form and coefficients of the models may differ for clones and for trees experiencing varying competition gradients. One of the objectives of this research was to investigate this conjecture.

2.5.2 Needle mortality within juvenile crowns

One of the important input variables in canopy production models is loss of leaf area (Pook 1984, Landsberg 1986) in time and space. Tree foliage may die due to aging processes (natural senescence), shading from other foliage and stress (water, space and light) (Dale 1982). A number of researchers have developed canopy production models (e.g. Kinerson *et al.* 1974, Pook 1984, Landsberg and Waring 1997, Waring and Running 1998). However, leaf area losses were estimated using needle litter fall (e.g. Rook *et al.* 1987, Kinerson *et al.* 1974, Pook 1984, Dalla-Tea and Jokella 1991, Raison *et al.* 1992a). Litter fall underestimates actual leaf area losses both in time and space, however (Raison *et al.* 1992a). This calls for more accurate methods of quantifying leaf area losses to be devised.

In this study better estimates of leaf area losses were achieved by putting up needle mortality sampling units in various parts of the tree crowns and physically counting needle losses.

2.6 PLANT GROWTH ANALYSIS

The foundations of plant growth analysis were laid down in the early part of the 20th century. The approaches used in this early part of the century largely involved fitting curves to data. The use of sound mathematical approaches became available in the late 1960s following advances in the field of statistical theory and experimentation. The availability of powerful electronic computers further enhanced data analyses procedures and allowed fitting of complex non-linear functions to growth data.

2.6.1 Growth and Relative growth rate

Growth is the permanent increase in the number of cells and size of an organism due to changes in physiology and morphology within the organism (Causton and Venus

1981, Hunt 1982). The rate of change with time is termed growth rate. Mathematically, growth is expressed thus:

$$Growth = W_2 - W_1 \qquad (2.16)$$

where W_1 and W_2 are size at times 1 and 2 respectively; while growth rate is expressed as;

$$Growth\ rate = \frac{change\ in\ size, (dW)}{change\ in\ time, (dT)} \qquad (2.17)$$

Relative growth rate (RGR), on the other hand, is defined as the ratio of the growth rate of an organism to its size at the beginning of the growth period. It is expressed mathematically as;

$$RGR = \frac{dW}{dT} * \frac{1}{W} \qquad (2.18)$$

Briggs *et al.* (1920) first used the term relative growth rate, although Blackman (1919) had used the idea previously under the name "efficiency index". RGR was used for agricultural crops. Only recently has it found wide applications to forestry trees (Causton and Venus 1981). This was mainly because forest trees remained in the field longer and the resultant changes in allometry as trees aged led to decreased RGR (Britt *et al.* 1991, Mason *et al.* 1996a). Moreover, prolonged exposure to the environment affected growth of different plant parts differently.

RGR is an instantaneous measure and therefore the mean between two growth periods is used. Mean relative growth rate is calculated using the formula, $\overline{RGR} = \frac{\ln(W_2) - \ln(W_1)}{T_2 - T_1}$ (2.19) (Hunt 1982, Evans 1972).

where, ln = logarithm and W_1 and W_2 = size at time T_1 and T_2 respectively.

Relative growth rate can be expanded into unit leaf rate (ULR), leaf weight ratio (LWR) and specific leaf area (SLA) (Evans 1972). ULR shows the dry matter conversion per leaf area ($ULR = \frac{dW}{dT} * \frac{1}{LA}$ (2.20)), while LWR shows the proportion of total dry matter allocated to foliage ($LWR = \frac{Lw}{W}$ (2.21)). SLA,

on the other hand shows how the foliage dry matter has been used to manufacture the radiation intercepting surfaces or leaf area ($SLA = \frac{LA}{Lw}$ (2.22)).

SLA and LWR together make up leaf area ratio ;

$$LAR = \underbrace{\frac{LA}{Lw}}_{SLA} * \underbrace{\frac{Lw}{W}}_{LWR} = \frac{LA}{W} \qquad (2.23).$$

Leaf area ratio is defined as the ratio of total tree leaf area to tree dry weight. It shows the proportion of dry weight in the form of leaf area.

This study sought to quantify plant allocation patterns to above ground components. Changes in leaf area, leaf weight and total biomass were quantified as functions of time and tree size. The reasons why relative growth rate diminishes with tree size and age in young trees before canopy closure were investigated by studying changes in ULR, SLA, LWR and LAR over 3 years.

2.7 GROWTH AND YIELD MODELLING

2.7.1 Introduction

A model is an abstraction of reality based on mathematical or logical assumptions (Christian 1975) about the current knowledge of the behaviour and/or working of a real system under different conditions (Landsberg 1986). Models should be formulated in precise statements. They should incorporate all the important relationships and entities of the "real" system and yet be simple enough to allow easy understanding and efficiency. By simplifying the operational relationships of complex systems, into simple understandable units, models help to achieve the following:

1) describe and understand complex real situations and thereby augment knowledge;
2) generate hypotheses and test validity of assumptions; and hence
3) optimize decision-making by revealing the nature and functional structure of poorly understood systems.

Mathematical models are preferred to conceptual or diagrammatic models, because unlike the latter, the former can be objectively derived and allow rigorous statistical hypotheses testing.

In forestry, growth models usually comprise statistically derived equations describing empirical growth data from experiments or permanent sample plots. This framework of equations helps researchers to understand the processes of tree growth (Goulding 1986, 1995) in response to management and silvicultural inputs including responses to environmental disturbances. The models are integrated into computer algorithms and are easily accessible to managers. Moreover, because forest trees are biological organisms, growth and yield models should not only be statistically sound but also make biological sense (Vanclay 1994).

Quantitative growth and yield models are therefore important prerequisites to sound management of forest resources (Burkhart *et al.* 1981, Clutter *et al.* 1983, Vanclay

1994). Well-developed growth and yield models can give accurate predictions of volume, value or weight of fibre and guide the decision-making process so that optimal decisions commensurate with management goals can be made (Clutter *et al.* 1983, Davis and Johnson 1987, Bailey and Ware 1983). Models can assist managers to plan in advance what the effects and outcomes of their decisions will be (Garcia 1988, Vanclay 1994). Moreover, growth and yield models, when appropriately developed, can give insight regarding for example, planting densities, thinning schedules and rotation ages of tree crops.

Models are developed for various reasons and uses. According to Blake *et al.* (1990) the usefulness of a model will ultimately depend on:

1) how well the modeller understands the basic structural and functional relationships of the system of interest;
2) the quality and quantity of data available, gathered using valid statistical methods to enable parameter estimation; and
3) the basic form of the quantitative expression in a predictive and testable format.

Additionally, an understanding by the modeller of how the model(s) will be applied and by whom (a small enterprise, a multinational corporation or a government agency) can result in wide acceptance of the model(s). It should be appreciated that growth modelling is an "art beyond the mere descriptive simplification of experimental data"; it is a vital research component forming an important facet in formalising structure of theory and hypothesis.

2.7.1.1 A brief historical perspective of growth and yield modelling

The development of formalised methods of describing forest data (modelling techniques) dates back to the early 1900s. Before the advent of current modelling techniques, managers relied heavily on local experience. However, this valuable knowledge was lost when a person retired. The effects of different management alternatives, for example, could not be estimated without a lot of human errors chiefly from memory lapses or lack of knowledge/experience. Drawing up a data bank of past experience and knowledge relating to different management and silvicultural options, as is the case today with the advent of powerful computers, was

of major concern. Additionally, the development of quantitative and statistically sound methods to enable unambiguous growth and yield forecasts was also viewed to be critical for sound management of the forest resource.

Official records of formalised description of forest growth therefore, started with the development of yield tables. Yield tables were graphically drawn using data from temporary plots. These "normal" yield tables gave the yield per unit area from "fully stocked stands" or "normal forests" (Husch *et al.* 1982, Clutter *et al.* 1983).

However, the normality concept was subjective and most stands had less than normal stockings. This led to the development of empirical yield tables (Husch *et al.* 1982, Clutter *et al.* 1983) using average stocking measures from random samples to cover various ages. The problem was that the empirical tables were insensitive to density variations and were of limited application. As a result variable density yield tables, which were applicable to stands with variable densities, were developed.

2.7.1.2 Forest stands as ecological entities

An even-aged forest stand comprises a group of trees exhibiting uniformity of age, treatments and by extension, growth habits. A forest stand can therefore, be regarded as an ecological entity with resource needs for example space, light, water and nutrients. Consequently, growth and yield functions should have a sound biological basis. Implicit in most forest growth and yield models are measures of growth processes and other factors which influence tree growth. Realistic models should therefore, integrate edaphic and weather variables (Woollons *et al.* 1998).

2.7.2 Types of growth and yield models

In forestry, the main uses of models are growth prediction, harvest planning, silviculture-, ecological and environmental- research (Alder 1980). In intensively managed exotic plantations in particular, managers use models to guide their actions and to enable them meet their objectives. The management objectives may include growth prediction, survival trends and planning of silvicultural operations, for

example fertilization, pruning, thinning and harvesting. Consequently, a variety of models exist for different uses, crop species, sites and ages. Some models are used for predictive purposes (e.g. those used to model forest growth). Other models are used to link up existing gaps in knowledge (e.g. process models) and are called models of understanding (Vanclay 1994). Models can either be deterministic or stochastic. Deterministic models do not incorporate any probability of future occurrences of unforeseen events and always give the same solutions for a given set of initial values. Stochastic models, on the other hand incorporate some probability function for future unexpected events. They therefore tend to end up with different solutions from multiple simulations with the same initial conditions.

Process models, also known as physiological or functional models, try to simulate the biological processes that lead to the production of biomass through photosynthesis. They employ measures of CO_2 concentration, nutrients, moisture and light levels as the main input variables (Landsberg 1986, Bruce and Wensel 1987, Bruce 1990, Vanclay 1994). It is important to note however, that all models tend to be empirical in form as they rely on periodic measurements of data. Thus the different model types tend to form a continuum. This is opposed to the common belief that the different groups have no similarities, or that process models are not empirical (Adlard 1995).

Clutter *et al.* (1983), Burkhart *et al.* (1981) and Davis and Johnson (1987) concur that models can easily be classified using the target population for which the models are developed and their intended uses (Bruce and Wensel 1987). In this regard, the emphasis, sensitivity and detail of out-puts desired are very important. This classification is useful particularly nowadays when sundry silvicultural and management approaches, modelling methodologies, and in particular the availability of powerful computing machines, are used. For example, regular intensively managed forest stands will require different model formulations to those used for irregular or less intensively managed stands. Moreover, management decisions may concern individual stands, entire forests to large regional forest resources necessitating use of different model forms.

Three main groups of growth and yield models are considered, based on the inputs and outputs generated. These are whole stand models, diameter distribution models and individual tree models (Burkhart *et al.* 1981, Clutter *et al.* 1983, Davis and Johnson 1987). Further, the individual tree models can be grouped into two: 1) those that require distances from neighbours as input variables (distance dependent) and 2) those that do not (distance independent).

2.7.2.1 Salient features of the main model types

The following table summarises the salient features of whole stand, diameter distribution and individual tree models (Burkhart *et al.* 1981, Clutter *et al.* 1983).

Table 2.1: Salient features of the main model types.

Charact-eristics	**Whole stand models**	**Diameter distribution models**	**Individual tree models**
INPUT	1. Use stand level variables, i.e. age, site index, basal area and number of stems per hectare.	1. Use stand level variables.	1. Need detailed data on each individual tree. Individual tree growth is simulated and summed up to give total yield/ha.
	2. Use available inventory data and are computationally efficient.	2. Use a probability density function (pdf- the weibull is popular) to estimate number of trees by diameter classes.	2. Annual growth simulated as a function of size, age and index of competition. - A random function adjusts growth for genetics and microsite differences.
	3. High powered equipment is optional.	3. High powered equipment is optional.	3. Need high powered computational equipment.
OUTPUT	1. Do not give information about size class distributions.	1. Give detailed size class information.	1. Give detailed information on stand dynamics and structure plus volume by size class distribution.
	2. Outputs not useful in evaluating various utilization options.	2. Alternative management options can be evaluated.	2. Quite flexible for evaluating different end use options.
	3. Less useful in analyzing a wide range of stand treatments.	3. Slightly informative for evaluating a range of treatments.	3. A wide range of stand treatments can easily be evaluated.
COST	Low for comparable outputs.	Moderate for comparable outputs.	Expensive due to nature of input data, equipment needed and running time.

2.7.3 Bottom-up and Top-down models

Bottom-up models are mechanistic in nature i.e. they are formulated based on the perceived functional mechanisms of the system(s) under study. Basic growth driving variables are used as the input for more complex physiological models. For example, detailed leaf photosynthesis, daily water use and light interception sub-models may be used in building a carbon-partitioning model for tree growth. Top-down models on the other hand, start with the "whole" stand or tree and slowly include detailed sub-models of the processes, as relevant information becomes available. For this reason, top-down models may be of immediate value in forest management (Landsberg 1986, Mohren and Rabbinge 1990).

In top-down models 3 factors are crucial (Mohren and Rabbinge 1990).

2.7.3.1 Growth determining factors

Examples of growth determining factors are tree physiology, temperatures and solar radiation. These factors set the upper limit of primary production. Intercepted radiation and foliage C-fixation efficiency determine the primary production in a stand.

2.7.3.2 Growth limiting factors

Growth limiting factors include site conditions, especially water and nutrient availability which influence attainable levels of production. Water supply and/or nutrients below the minimum requirement levels (for site and species) will retard growth.

2.7.3.3 Growth reducing factors

Factors that reduce growth impact on the potentially achievable levels of production. Incomplete canopy closure, pests, weeds and diseases can result in growth below that potentially accruable at a site.

2.7.4 Quasi-process or Mixed models

Another group of model classification is the "mixed"- (Blake *et al.* 1990) or "phenomenological"- (Adlard 1995) or "Quasi-process"- models (Landsberg 1986). These models encompass both functional and predictive elements. Growth modifiers used in these models estimate the effects of the driving variables. For example competition, moisture, N_2-cycling, radiant energy capture and pollution can be included in the modifiers. Phenomenological models, if well formulated have the potential to facilitate the understanding of low level processes essential for tree growth in different environments (Landsberg 1986, Blake *et al.* 1990) and can be useful tools in integrating knowledge quantitatively. With the ever changing chemical environment (e.g. increasing CO_2 levels) and global climate change, "static" models developed using data accrued from long-term experiments and using yield as the independent variable may incur considerable bias in predictive power (accuracy and precision) (Fosberg 1990). Models which use physiological processes as the building blocks, may be more robust and applicable to variable growth conditions (Landsberg 1986, Adlard 1995).

2.7.5 Restricting model choices

With the availability of powerful computers there is a danger of developing very complicated models. Simple models however, are to be preferred to complicated models because complicated models: 1) demand a lot more computational time hence are more expensive; and 2) may give less precise estimates as a result of many variables' inclusion (Bruce and Wensel 1987). Another short-coming of models with many variables is their impracticability; i.e. they may not be easy to adopt in real life situations because of the difficulty in assessing some of the input variables and/or cost of carrying such exercises satisfactorily.

Bruce and Wensel (1987) and Burkhart *et al.* (1981) listed some of the important guidelines to consider when choosing models as:

1) reliability of the estimates;
2) malleability to reproduce needed management alternatives;
3) sufficiency of detail for decision-making needs;
4) efficiency with which desired information can be produced;
5) levels of details required; and
6) management practices in use.

When developing models, modelers need to consider the end users and the cost of gathering relevant input data (Whyte 1994). The way the models will be used, the operational costs (machine time and operator qualification) are also important considerations. There is little use in producing complex models which may never be used (or can be used but improperly) due to social-cultural, economic and political hiccups. These requirements are in addition to the more common ones, for example statistical reliability of the outputs, biological conformity and soundness of the equations to the growth processes being described. Care should also be exercised to see that estimates are within reasonable limits of observed variables (Bruce 1990). Information on the character of the database used to build the models and the assumptions used are also helpful.

2.8 EARLY GROWTH MODELLING

2.8.1 Overview

Initial or Early growth models are systems of equations which predict the yield and survival of juvenile tree crops prior to canopy closure. The models use nursery management information, stock type and site factors (rainfall, temperatures, incidence of frosts, altitude) as inputs. This information is integrated with pre-planting site management data and post-planting site management data to come up with survival and growth trajectories of young crops normally up to age 5 (Belli and Ek 1988) when canopy closure occurs (for radiata pine in the Central North Island of New Zealand, (Mason 1992)). Examples of pre-planting site management

information are site preparation methods, weed species and growth habits and mineral nutrient status of the site. Examples of post-planting site management information are weeding type and frequency and nutrient amelioration. Thereafter, later growth models are used up to crop harvesting age. Initial growth models are important as they give useful insights to managers regarding stock selection, nursery regimes and weed control options best suited to the sites where afforestation or refforestaion is to take place.

Belli (1987), Payandeh (1987) and Belli and Ek (1988) modelled early growth of conifers in the great lake states in the Western USA. In New Zealand the growth of radiata pine from planting to age 5 has been modelled by Mason (1992), and Mason and Whyte (1997) for the Central North Island and Zhao (1999) for Canterbury in the South Island.

Mason (1992), Mason and Whyte (1997) and Zhao (1999) developed models that were sensitive to site preparation, altitude, weeding, fertilization, rainfall and their interactions using dummy variables. What's more, the models by Mason (1992) were integrated into a decision support system (DSS) which allowed managers to select stock type, and post-planting site management alternatives (e.g. weeding and fertilization). While the models developed by these researchers sufficed, they described growth of trees growing in conditions which were either completely weed-free or completely weed-infested. In practice, managers maintain some form of weed control (Evans 1992, Chapman and Allan 1978). Genetic effects were not included in the models by the three authors as well. Therefore, there is an urgent need to develop models that are sensitive to situations of varying weed competition and different genotypes.

2.8.2 Need to quantify early growth and survival

Initial growth models are important in forestry plantation establishment. The future success of any forest venture relies on how well the juvenile crops establish (Sutton 1991) and consequently grow to maturity (Mason 1996). Once seedlings have

recovered from transplanting shock their chances of survival to canopy closure and maturity may greatly increase, subject to post-site management and the weather. Accurate and reliable Initial Growth Models ensure that managers have a sound and reliable basis for making decisions about the young growing stock within known probability levels.

Accurate early growth models could assist managers to develop reliable schedules for future silvicultural and management activities, for example weeding frequency, fertilization, time to first pruning and thinning and final crop tree selection. Without reliable quantitative models managers would be left at the mercy of uncertainty, depending on subjective "beliefs" and experiences from "rules of thumb". Mason (1992) and Mason and Whyte (1997) listed the following salient features of initial growth models:

1) there is no significant intra-specific competition at the initial stockings used in New Zealand (800 - 1200 stems per ha);
2) growth processes are before current annual increment peak;
3) micro-site environment may influence growth significantly;
4) pre-plant management practices (site preparation) may have significant effect on growth and survival;
5) site quality is of little importance to initial tree size compared to later ages when it can significantly influence growth and tree survival; and
6) pre-plant factors particularly nursery regime, lifting and planting quality can have profound effects on growth and survival immediately following planting.

One of the aims of the study described here was to develop provisional models of young crops incorporating the effects of different genotypes and weeding gradients. There is need to further refine estimates of weed influences in current initial growth models. This thesis reports research directed towards that need as well.

2.8.3 Summary

Some researchers have noted that the "success" of establishment practices is best judged at the end of the rotation (e.g. Mason 1992) because some growth trends resulting from some of the management inputs at this stage (age 1 to 5) are short-lived. For example, weeding has been reported to offer temporary benefits i.e. type I response (Snowdon and Khana 1989, Mason and Milne 1999). Furthermore, the "success" depends on the criterion used by managers. For example, Belli (1987) found there was a reversal of "success" rating depending on whether cost/1000 seedlings or aggregate height was used as the criterion.

This not withstanding, the cost, survival and growth rate of the crops are sufficient guidelines for evaluating the success of the establishment phase and early growth models can be used reliably to assess marginal expenditure. What-is-more, the future growth trends of a plantation can be guided reliably by the application of informed, objective management and silvicultural techniques. It is almost impossible for a manager, however diligent, to salvage a plantation and turn it into a successful venture if the establishment was a total failure. On the other hand, a very well established plantation with high growth rates and survival can fail completely to meet the desired end products if poor management and silviculture are used. It may suffice to say that while the overall performance and profit margins are best judged at the end of the rotation, the success of the establishment phase need not wait up to the end of the rotation to be accredited.

In summary, initial growth models ensure that managers have:

1) readily available tools and information pertaining to plantation establishment to enable sound decision making;
2) initial datum point(s) for a combination of pre- and post-plant site management alternatives using different planting stock and/or genotypes;
3) consistent systems of comparing and contrasting the outcome from various possible establishment scenarios to suit a multitude of desired management objectives; and

4) reliable tools to increase sensitivity analyses of treatment effects, for example various weeding treatments, clones and their interactions.

CHAPTER 3

SYNOPSIS OF THE EXPERIMENT

A genotype-by-weed competition experiment was set up in September of 1996 at Dunsandel, South of Christchurch city on the Canterbury plains of the South Island, New Zealand. The experiment had four levels of weed competition and seven clones of radiata pine (*Pinus radiata* D. Don).

3.1 SITE DESCRIPTION AND MAIN WEED SPECIES

The site was flat with Lismore Stony Silt Loam soils. Average annual rainfall at the site was 600 mm with most of the rain falling in the winter months (May to August in New Zealand). Mason and Kirongo (1999) reported unusually low rainfall during the second growing season (1997-1998) at the site. The site had previously been under pasture and grasses were the dominant weeds. The most abundant pasture weeds were Italian ryegrass (*Lolium multiflorum*), white clover (*Trifolium repens*), and sorrel (*Rumex acetosella*).

3.1.1 Growth form and habits of main weed species

3.1.1.1 Italian ryegrass (*Lolium multiflorum* Lam.)

Italian ryegrass is an annual bright green pasture grass, which grows up to 1.2 m tall. It has characteristic large auricles and awns (3 - 15 mm long) which distinguish it from other closely related *Lolium* species, especially *L. perenne* with which it hybridises readily (Lambrechsten 1992). Leaf blades can be up to 30 cm long with smooth lower surfaces. *Lolium* spp. are aggressive weeds. At maturity they bear terminal inflorescence. They can be killed readily during the early stages of growth

(Auld and Medd 1987, Matthews 1956). In New Zealand Italian rye grass is commonly found on moist soils and pasture sites (Lambrechsten 1992).

Italian ryegrass has been reported to show allelopathic effects especially in mixture with pampas grass (Ray and Richardson 1993, Gadgil *et al.* 1990). Allelopathy can be defined as the production of chemical exudates by one plant to inhibit the growth of another sharing the same micro-environment. No measurements of possible allellopathic effects by ryegrass were undertaken in this study.

3.1.1.2 White clover (*Trifolium repens* L.)

Originally from Europe, north Africa and north and west Asia, white clover is now abundantly distributed in New Zealand. White clover is a perennial, hairless weed which grows up to 30 cm tall. It has 3 roundish leaflets with v-marks on the surface (Roy *et al.* 1998). At maturity white clovers have white to pinkish/red flowers 8 to 12 mm long grouped into 'heads' which are 1.5 to 3 cm in size. Clovers have massive fibrous root systems and are commonly found in pasture, lawns, road sides and even river beds (Parham and Healy 1976, Roy *et al.* 1998).

3.1.1.3 Sorrel (*Rumex acetosella* L.)

Sorrel, commonly known as sheep's sorrel, was originally brought from Europe. It is now a common weed in New Zealand especially in cultivated, waste land, pasture and grassland areas. Sorrel is a perennial semi-erect weed which grows to a height of 30 cm. It is rhizomatous with yellowish roots spreading far and colonising wide areas with its adventitious buds (Roy *et al.* 1998). The hairless arrow-shaped leaves have an acidic taste. At maturity it bears red flowers. Sorrel is tolerant to most hormone-based herbicides (Parham and Healy 1976, Roy *et al.* 1998). The presence of sorrel may indicate a 'sour' (alkaline) soil.

3.2 EXPERIMENTAL DESIGN AND LAYOUT, TREATMENTS AND MAINTENANCE

The experimental design used was a randomised complete block design with three replications in a split-plot layout. The main plots were made up of four weeding treatments:

1) complete weeding equivalent to 9 m^2 of weed-free area around each tree, Wc9;
2) weed free spots equivalent to 3.14 m^2 of weed-free area/tree, Wc3[1];
3) weed free spots equivalent to 0.75 m^2 of weed-free area/tree, Wc0.75; and
4) weed free spots only at time of planting equivalent to 0.03 m^2 of weed-free area/tree, Wc0.03.

These weeding treatments represented a 3-by-3 m^2 area and spot-diameters of 2, 1 and 0.2 m respectively.

The main plots were laid out randomly and measured 36 x 27 m. Ten individuals of each of seven clones were planted in single lines in each plot i.e. 70 individuals per plot. Planting lines were ripped to a depth of 30 cm before planting. Planting spots were centered on the planting lines at an espacement of 3 x 3 m. A guard row of GF12 (growth and form factor - see clonal forestry section 2.2.2 in chapter 2) seedlings surrounded all the plots. Trees in the guard rows were subjected to similar weeding treatments as those of the plots they surrounded.

3.2.1 Clonal material

Ten individuals of each of seven clones, designated Cl_1 to Cl_7 formed the sub-plots. The clones were donated by the Fletcher Challenge Centre for Biotechnology. All the clones were from different parents. Embryos of control pollinated seed were used to produce the clones. The embryos were cold-stored (cryogenic storage) to discourage maturation and thereafter multiplied using organogenesis. The resultant plants were

[1] This weeding treatment appears as 3.00 in graphs.

conditioned by under-cutting and wrenching and then hardened-off before lifting and planting.

3.2.2 Weeding

In this study, weeds were controlled using chemicals (herbicides). The weeding gradients were maintained using circular plastic guards to surround treated plants during spraying. This ensured that exact 1 and 2 m spots were achieved and reduced chemical drift to neighbouring seedlings and other vegetation. For the complete weeding treatment, a boom mounted on the wand of a knapsack sprayer was used.

Terbuthylazine (7.5 kg of active ingredients, a.i.), 300 g (a.i.) haloxyfop plus 900 g clopyralid were added to water and the mixture was applied at a rate of 250 L/ha. Sorrel was not completely killed by this mixture, however and an additional 3.75 g (a.i.) of tribenuron methyl and 36 g (a.i.) of oxyflourfen was used to bring it under control.

3.2.3 Herbicide application frequency

The control plots (Wc0.03) were sprayed only once 3 weeks after planting. All the other treatments were sprayed 3 weeks after planting and subsequently whenever necessary to thwart any weed resurgence.

3.2.4 Weather variables

Weather variables especially rainfall amount and distribution and solar radiation data could be important inputs into canopy production models. However, in this study it was not possible to collect rainfall or solar radiation data on site. Mean rainfall and temperatures from the weather station nearest to the site is in the appendix.

3.3 OVERVIEW OF SPECIFIC STUDIES UNDERTAKEN

The following sections give an overview of the main aspects of this study. Subsequent chapters will describe the methodology in more detail and present the findings.

During this study crown foliage budgets of 3-year-old radiata pine clones growing under variable weed micro-environments were evaluated. Leaf area and specific leaf area spatial distribution as well as fascicle mortality in time and space were quantified. Changes in mean relative growth rate ($\overline{RGR}$) were evaluated by quantifying the morphological and physiological terms of the RGR expansion (equation 3.1). Provisional models of height and basal-basal area integrating weeding and clonal effects were also developed.

Crown foliage budget studies aimed to evaluate foliage changes by tree age or size in different clones. Specifically, the additions of new foliage and losses due to natural mortality (senescence) and/or browsing and the effects of weed competition were monitored. In order to achieve this, estimates of crown leaf area were made using image analysis. The estimated leaf areas were adjusted for losses due to needle mortality using data from needle mortality studies.

Data from limited destructive sampling of trees set aside for this purpose at the onset of the experiment were used to fit functions of crown area in photos measured using image analysis vs. tree leaf dry weight and total tree biomass. Leaf area spatial distribution data from standing trees was used to fit general functions for leaf area versus leaf dry weight. Crown photo areas of standing trees were used to calculate total tree leaf areas using the leaf area vs. leaf weight relationship and the crown photo areas vs. tree leaf weight regressions.

The estimated total tree biomass, leaf weight and leaf area were used to compute the values of the terms in the RGR expansion (Evans 1972);

$$RGR = \underbrace{\frac{dW}{dT}}_{ULR} * \underbrace{\frac{1}{LA}}_{} \times \underbrace{\frac{LA}{Lw}}_{SLA} \times \underbrace{\frac{Lw}{W}}_{LWR} \qquad (3.1)$$

RGR changes with time and tree size were evaluated. The effects of weeding and genotype on RGR were also evaluated. During the third growing season, needle growth rates were measured and related to direct soil moisture measurements in the total weeding and control plots. Detailed discourse on the methodology used in each of these studies is presented in the relevant sections.

3.4 MEASUREMENT FREQUENCY

Height, GLD, tree survival, limited destructive sampling, needle survival counts, crown area photos measurements, crown structure, leaf area and specific leaf area data were taken in winter (May to August) of each year. Some height measurements were taken in summer and these were adjusted for seasonal effects as recommended by Zhao (1999). Needle elongation and soil moisture measurements were taken only during the 3rd summer. All tests of significance were carried out at $\alpha = 0.05$ probability level.

3.5 DATA ANALYSIS PROCEDURES

Models are based on assumptions about the 'true' functioning of the 'real or actual' system. The more accurate the assumptions are in describing the true functioning of the system and the more reliable the data used, the better the model outputs will be and the lower the residual errors. Thus, fitted models of tree growth rely heavily on:

1) data collected; and
2) *a priori* assumptions made regarding tree growth and the processes driving growth.

Once the data have been collated using statistically valid methods to enable hypothesis testing, biologically sound assumptions describing the functioning of the

system being modelled, as closely and accurately as possible, must be used in formulating the models. Relaxation of some assumptions is sometimes inevitable. However, care should be exercised to avoid gross oversimplifications and/or unnecessary extrapolations beyond the capacity of the data.

In this study, plots of the dependent versus independent variables were made using GPLOT procedure in SAS (SAS/STATS 1996) before fitting any models. The general trends in the plots were used to show the behaviour of the variables and were used to identify relevant candidate model formats. The SAS statistical package (SAS/STATS 1996) was used in analysing the data. For example, the regression procedure (Proc REG) was used to relate fascicle mortality to measured tree crown variables while the logistic procedure was used to identify variables which explained tree survival to a higher probability. The general linear models procedure (Proc GLM) was used for analysis of variance (ANOVA). Significant variables and their interactions were subjected to specific hypothesis tests using the appropriate plot and subplot error terms. The Tukey option of the GLM procedure in SAS was used to identify specific weeding treatments or clones that differed significantly. The non-linear regression procedure (Proc NLIN) was used to fit non-linear functions to data, for example height, basal-basal area and tree survival models.

Final models were chosen based on the normality, precision and lack of bias in the residual plots. Of particular importance in the residual plots were lack of definite trends and tightness, close to the zero line. Models with small mean square error of residuals (RMS) were tentatively selected. Rigorous scrutiny of plots of residuals by predicted and all independent variables was then used as the major criterion. This is because the analysis of residuals, especially using plots, is a powerful technique which helps identify any outliers or anomalies in variance or if transformations are needed (Weisberg 1985, Draper and Smith 1966, Cook and Weisberg 1982). Measures of skewness (tendency of the residuals to be larger to the left (-ve) or right (+ve)) and kurtosis (heaviness of the tails) were also used. Skewness is unbound while kurtosis should be greater than -2. However, kurtosis values greater than 4 were investigated further.

CHAPTER 4

MODELLING MEAN HEIGHT, BASAL-BASAL AREA AND MORTALITY

4.1 INTRODUCTION

The importance of the establishment phase to the future viability of the plantation venture has been well discussed by many researchers (e.g. Belli and Ek 1988, Sutton 1991, Evans 1992, Mason 1992, Mason and Whyte 1997).

In New Zealand successful establishment of radiata pine plantations is influenced by pre- and post-plant factors. Examples of these factors are stock type (e.g. Mason *et al.* 1996b, Mason -in prep.), stock quality (Chavasse 1980, Trewin and Cullen 1985, Menzies 1988), land preparation (Mason and Cullen 1986, Mead 1990), handling (Balneaves and Menzies 1990), genetics (Mead *et al.* 1993, Burdon 1995) and planting quality (Mason 1985). Plant nutrition (Mead *et al.* 1984, Mead 1990, Maclaren 1993) and timely release from competing non-crop vegetation (Mason 1992, Balneaves and Clinton 1992, Richardson 1993, Mason *et al.* 1996b, Kirongo 1996, Mason and Kirongo 1999) are also important to ensure successful establishment and maintain crop vigour. Some methods of site preparation, for example the use of heavy machinery, can have negative impacts, while the use of fire can degrade a site (Maclaren 1993).

These observations are consistent with results from studies done elsewhere, especially regarding fertilization (Snowdon 1985, Snowdon and Waring 1985), genetics (Evans 1992), and weed control (Squire 1977, Nambiar and Zed 1980, Wagner *et al.* 1989, Evans 1992, Sands and Nambiar 1984, Nambiar and Sands1993).

Decisions taken by managers during establishment can have significant effects on future growth trends and profit margins. Managers therefore need quantitative information in a ready-to-use format to aid efficient and correct choice of silviculture and management strategies (Mason 1996, Mason and Whyte 1997). Models of juvenile tree growth patterns that are well formulated and incorporate a variety of management and silvicultural treatments are an invaluable management tool. Moreover, integrating the models into a DSS is a way of empowering managers in their decision-making processes regarding establishment treatment choices (Mason 1992, Mason 1996).

4.1.1 Height models

Tree growth during the first five years after out-planting (juvenile phase, insignificant between-tree competition) is strongly related to size. Trees with larger crowns have more leaf area and in the absence of any stress (competition, moisture, nutrients) will maintain higher absolute growth rates. Growth is exponential and can be expressed mathematically thus:

$$\frac{dY}{dT} = \alpha * Y^{\beta} \qquad (4.1)$$

where $\frac{dY}{dT}$ is the rate of height change with respect to time, Y = tree size (height) and α and β are regression coefficients. Solving this equation and integrating between 0 and Y and 0 and T gives:

$$Y_T = \gamma * T^{\delta} \qquad (4.2)$$

where;

$$\gamma = \{(1-\beta) * \alpha\}^{\left(\frac{1}{1-\beta}\right)} \qquad (4.3)$$

and

$$\delta = \frac{1}{1-\beta} \qquad (4.4)$$ (Mason 1992).

Belli (1987) and Belli and Ek (1988) modelled the mean height of white spruce (*Picea glauca*) and red pine (*Pinus resinosa*) in the Lake States (USA), using the same exponential function. However, as Belli and Ek (1988) pointed out, planted trees unlike trees regenerated in situ have a positive height (and diameter) at time of planting and, therefore the models fitted should have an intercept equal to the mean height at planting. The function therefore becomes:

$$H_T = H_0 + \gamma * T^{\delta} \qquad (4.5)$$

where;

H_T is height at time T, H_0 = initial tree height, T = tree age (time), γ and δ are coefficients.

Mason (1992) and Zhao (1999) used the function to model the mean height of juvenile radiata pine in New Zealand. Mason (1992) modelled the initial growth of radiata pine in the Central North Island of New Zealand while Zhao (1999) modelled the juvenile growth of radiata pine in Canterbury in the South Island of New Zealand. Both Mason (1992) and Zhao (1999) developed models that were sensitive to site preparation, altitude, weeding, fertilization and their interactions using dummy variables.

4.1.2 Basal-basal area models

Many modellers of initial growth of conifers did not model basal area because diameter at breast height (dbh = diameter at 1.40 m above ground in New Zealand and 1.30 m in other countries) is undefined in young trees (e.g. Payandeh 1987, Belli and Ek 1988). However, because the juvenile growth phase covers the first 5 years following out-planting, it is actually possible in some cases to have one- or two-years' dbh data. Mason (1992) noted that modellers used a 'relative growth modifier' (RGM) in basal area models with the aim of 'transforming' the basal area function from an exponential to a sigmoidal function. Thus basal area growth with respect to time was expressed as:

$$\frac{dG}{dT} = f(G, RGM) \qquad (4.6)$$

where;

dG/dT = basal-basal area change with time, G = basal-basal area, RGM = relative growth modifier and f = function of.

Mason (1992) debated at length the ramifications and theoretical assumptions behind such a function. He pointed out that at height 1.40 m basal area growth was assumed to be zero ($\frac{dG}{dT} = 0$), which was not sensible and concluded that a constant (k) describing the capability of the stand to grow when height was below 1.40 m needed to be included in the basal area models. This is because trees had noteworthy amounts of leaf areas. He therefore modified sigmoid equations to;

$$\frac{dG}{dT} = f((G + k), RGM) \qquad (4.7)$$

Mason (1992) went further and formulated an expression for k which he used to develop compatible basal area and height equations for juvenile crops.

4.1.3 Tree survival

Survival estimates are an important feature of growth and yield models (Burkhart *et al.* 1981). Tree survival may vary greatly with time. This added to the fact that mortality data is normally collected from small plots with few re-measurements makes tree survival one of the most challenging variables to model accurately (Glover and Hool 1979); sentiments that were echoed by others e.g. Woollons (1998) and Lee (1998). Good mortality equations can ensure that discrepancies between predicted and standing volumes are kept to a minimum.

In intensively managed monocultures mortality is assumed to be insignificant in comparison to natural mixed forests (Vanclay 1994). Mortality is usually related to some measures of competition or suppression. Tree size and age are used as the indicators of the probability of tree death. Mortality due to ageing, suppression and

competition may be treated as a natural phenomenon to differentiate it from that caused, for example by wild fires, lightning or cyclones (Vanclay 1994) which can devastate large estates.

Remeasured data from permanent sample plots (PSPs) is normally used to estimate mortality during a time period (T_2-T_1) using difference equations of the general form:

$$N_2 = f(N_1, T_1, T_2) \qquad (4.8)$$

where;

N_2 = number of stems at time T_2,

N_1 = initial number of stems at T_1,

T_1 = time at the start of the period,

T_2 = time at the end of the period (Clutter *et al.* 1983).

With the assumption that no in-growth occurs in even-aged stands, Clutter *et al.* (1983) list the following properties which the equations must satisfy:

1) consistency in form, i.e. if T_2 tends to T_1 then N_2 will equal N_1;
2) path invariance in predictions such that predicting N_3 from T_1 and N_1 is the same as predicting N_3 from N_2 and T_2 and N_1 and T_1;
3) as T_2 approaches infinity, N_2 tends to an asymptote; and
4) for any $T_2 > T_1$, N_1 is expected to be greater than N_2.

However, Woollons (1998) observed that this last property (4 above) was almost always contravened, especially in thinned plantations where no deaths may be recorded over a time period T_2-T_1.

4.1.3.1 Special characteristics of survival studies

Modelling mortality is similar in some respects to survival analysis. Survival analysis is useful in quantifying the numbers of organisms that survive during a certain time period (SAS/STAT 1996). In forestry the concern is the occurrence of mortality as the stand matures. If mortality is assumed to be the event of interest and the time until a tree dies the event time, then similar properties can be drawn. For example:

1) observations may be stopped before the actual event occurs (e.g. in growth plots no death may be recorded within the time period of the study); and
2) the response cannot be negative.

Modellers of tree survival need to use all the data, including intervals where no event (death) was observed (Woollons 1998). This has not normally been the case. Many previous researchers (e.g. Lee 1998, Temu 1992, Ngugi 1996) have modelled mortality by first screening their data to avoid modelling over intervals where no deaths have been observed. If no mortality occurred between T_1 and T_2 in a plot, but mortality occurred between T_2 and T_3, then only the T_1 to T_3 and the T_2 to T_3 intervals were included in the data set. While this was necessary to satisfy the assumption that for any $T_2 > T_1$, N_1 is expected to be greater than N_2 (i.e. $N_2 < N_1$), it resulted in over estimating mortality because for any $T_2 > T_1$, and where the actual $N_2 = N_1$ (i.e. no mortality was observed), N_2 was forced to be less than N_1. Woollons (1998) reported that models fitted with data that excluded intervals where no mortality had occurred, gave residual plots which were "visually more appealing".

Therefore, it should be borne in mind that the act of excluding intervals with no death introduces some bias because in most plantations it is normal to have time intervals with no mortality, especially in thinned plantations (Woollons 1998). So the bias arises from the removal of intervals showing no tree death rather than the model fitting process.

Woollons (1998) suggested a 2-step regression process involving:

1) fitting a logistic equation to all the data to estimate the probability of stems dying;
2) modelling mortality using difference equations but after screening to completely remove intervals with no deaths; and
3) adjusting predicted stems per hectare by the probability of mortality i.e. $N_{adj2} = N_1 - p*(N_1 - N_{pred2})$ (4.9).

N_{adj2} = predicted stems per hectare after adjusting using the probability calculated from the logistic procedure, N_I = initial stocking, p = probability of stem death and N_{pred2} = predicted stems per hectare from step 2.

The method can be used for regular and irregular intervals (Woollons pers. comm.). In this study survival counts were recorded annually and so regular 1-year intervals were used.

4.1.3.2 The Logistic procedure

The logistic procedure fits linear logistic regression models for binary or ordinal data using maximum likelihood method (SAS/STATS 1996). The relationship between the response probability and the explanatory variables is modelled by assigning p = 1 to the event of death occurring and p = 0 to the probability of no death. The model formulation is:

$$\log it\,(p) = \log\left(\frac{p}{1-p}\right) \qquad (4.10)$$

$$= \alpha_0 + \alpha_1 X_1 + \alpha_2 X_2 + \ldots\ldots + \alpha_n X_n \qquad (4.11)$$

where;

α_0 is intercept parameter and α_1 to α_n are slope parameters.

The logistic equation constrains the predictions within 0 - 1 and results in a binomial distribution of errors. The logistic model has a link function called the *logit* function (SAS/STATS 1996). The link function is such that a given function f = $f(\mu)$ of the mean of the response variable is linearly related to the explanatory variable.

4.1.4 Using dummy variables

Fitting of models can sometimes be enhanced by the inclusion of dummy variables. Dummy variables are useful for representing significant variations in parameter values between regions and/or treatments. In models of juvenile radiata pine in New Zealand Mason (1992), Mason and Whyte (1997) and Zhao (1999) made extensive

use of dummy variables to represent differences in site preparation, weeding (1 for weeding and 0 otherwise), and stock type. Temu (1992), while modelling Douglas fir growth in the South Island of New Zealand found dummy variables to be very helpful for aggregating regional differences in one model as opposed to fitting separate models for each region.

For example, in a simple linear regression involving 4 treatments, Wc_1, Wc_2, Wc_3 and Wc_4 a model assuming all treatments have slopes and intercepts that do not statistically differ significantly from each other is:

$$Y_{ij} = \alpha_0 + \beta_0 * X_{ij} + \varepsilon_{ij} \qquad (4.12)$$

where, α, β and ε represent the intercept, slope and error terms respectively. However, if statistical significant differences are observed for all the slopes and intercepts the model becomes;

$$Y_{ij} = (\alpha_0 + \alpha_1 * Wc_1 + \alpha_2 * Wc_2 + \alpha_3 * Wc_3) + \beta_1 * Wc_1 + \beta_2 * Wc_2 + \beta_3 * Wc_3 + \beta_0 * X_{ij} + \varepsilon_{ij} \qquad (4.13)$$

where,

Wc_1, Wc_2 and Wc_3 are dummy variables for any 3 of the treatments the fourth one is the default represented by α_0 and β_0. $\alpha_{1\text{-}3}$ and $\beta_{1\text{-}3}$ are the associated coefficients for the dummy variables 1-3 respectively.

Any $\alpha_{1\text{-}3}$ or $\beta_{1\text{-}3}$ which statistically do not differ significantly drop out and the model is scaled down to leave only statistically significant dummy variables.

The use of dummy variables avoids fitting a multitude of models or using various adjustment factors (Temu 1992). By carrying out hypothesis tests on the parameter estimates the need to have different models for different regions, genotypes, stock types or weeding treatments can be justified.

4.2 MODEL STRUCTURE

4.2.1 Mean height models

Mason (1992) found that the best equation describing juvenile radiata pine mean height growth was;

$$\overline{H}_T = \overline{H}_0 + \alpha * T^{\beta} \qquad (4.14)$$

where;

$\overline{H}_T$ = mean height at age = T,

$\overline{H}_0$ = mean height at planting time,

T = age when H_T was measured, and

α and β = estimated coefficients.

In the equation α is the rate coefficient while β is the shape coefficient. Different models will therefore ensue if;

1) the rate coefficient, α differs significantly between treatments/clones.
2) the shape coefficient, β differs significantly between treatments/clones, or
3) both coefficients (α and β) differ significantly between weeding treatments/clones.

4.2.2 Basal-basal area models

Before canopy closure basal-basal area growth can be represented by an exponential function, as trees are growing without any significant between-tree competition and growth processes are before the inflection point when the function changes from exponential to sigmoid. Basal-basal area can therefore, be expressed using the function:

$$G_{GL} = \alpha * T^{\beta} \qquad (4.15)$$

where, G_{GL} = Basal-basal area or basal area at ground level,

T = time or age and α and β are regression coefficients.

Basal area per hectare depends on stand density as well and thus the number of trees present. Hence an estimation of stem survival needs to be included in the function. To solve this problem the number of initial stems per hectare is included in the equation. This is plausible because managers readily have the initial stockings (number of stems per hectare, N_0) but may not have accurate predictions of mortality rates. The final basal-basal area equation would be;

$$G_{GLT} = \alpha * N_0 * T^{\beta} \qquad (4.16)$$

where N_0 represents the initial stocking levels and other variables are as defined earlier. Furthermore, basal-basal area at time of planting ($G_{GLT=0}$) is not zero and so the equation is constrained to conform to an intercept equal to basal-basal area/ha at time of planting. The equation then becomes:

$$G_{GLT} = G_{GLT=0} + \alpha * N_0 * T^{\beta} \qquad (4.17)$$ (Zhao (1999).

In this study, models in yield form were preferred for similar reasons as those observed by Mason (1992): when making decisions regarding establishment treatments at time of planting, managers usually have tree dimensions at planting rather than after growth has occurred on-site. Therefore, even though models in difference form may be more appropriate in investigating growth trends resulting from different levels of vegetation control, for example, such formulations (difference equations) can obscure true effects of competition behind initial size (Y_0) and time (T_0). This is because future size (Y_T) is highly correlated to initial size (Y_0) in difference equations.

4.2.3 Survival models

In juvenile plantations tree deaths are expected to decrease with time as the seedlings become established in their new environment and the effects of transplanting shock (stress) become diminished (Mason 1992). Moreover, as seedlings rapidly increase in height they grow away from the harsh environment close to the ground, especially temperature fluctuations which can cause further stress. Tree survival can be expressed using an exponential decay of the form;

$$S_T = \exp(-\alpha * T^{\beta}) \qquad (4.18),$$

where ;

S_T = tree survival, T= time and α and β are regression coefficients (Belli and Ek 1988, Mason 1992, Mason and Whyte 1997).

4.2.4 Summary

The importance of modelling height, basal-basal area and survival in this study arises due to the following reasons:

1) previous models had limited representation of weeding treatments (e.g. Mason 1992, had only two treatments; weeding or no weeding); and
2) growth of different genotypes subjected to varying weed gradients has not been modelled in New Zealand.

With the proliferation of establishment techniques and the move towards 'promising' genotypes (for better form, growth, disease resistance) it is useful to identify whether different genotypes can respond differently to varying cultural treatments.

4.3 METHODS

4.3.1 Parameter (coefficient) analysis

Models of height (equation 4.14) and basal-basal area/ha (equation 4.17) were fitted to each plot separately (i.e. by blocks, treatments and clones) and the coefficients output to a file. Analysis of variance using Proc GLM (SAS/STATS 1996) was used to test for significant differences in coefficients between weeding treatments and/or clones. The Tukey test was used to identify treatments and clones which were significantly different from each other at $\alpha = 0.05$.

The following procedures were followed.

1) The model with minimum residual error sum of squares and 'best' residual trends was chosen, e.g. $H_T = H_0 + \alpha * T^{\beta}$ for height.
2) Sub-models were fitted by weeding and clones. The parameters (α and β) estimated from the fit(s) were output to a file.
3) Means for the coefficients for each weeding and clone group were used to test if the differences between them were significant using GLM procedure in SAS.
4) The Tukey option (a multiple range test) in the GLM procedure was used to identify treatment and/or clone groups that differed significantly amongst each other.
5) The model was refit with the significant weeding and clone groups as dummy variables.
6) The dummy variables were put as linear terms of α and β in the revised model.

Plots of the coefficients versus weed free area/tree were plotted. Where a strong trend was evident between the coefficients and the weeding treatments then a model was fitted. The fitted model was then included as a linear term in the overall fit.

Final models were selected based on low root mean square error of residuals (RMS) and especially the normality and lack of bias in the residual plots (Weisberg 1985, Draper and Smith 1966, Cook and Weisberg 1982).

4.4 RESULTS

4.4.1 Mean height models

The final model for mean height was equation 4.14; $\overline{H}_T = \overline{H}_0 + \alpha * T^{\beta}$;

$\alpha = \alpha_0 + \alpha_1 * \log(Wc) + \alpha_2 * V_2 + \alpha_3 * V_4 + \alpha_4 * (Wc9 * V_4) + \alpha_5 * (BL_3)$

$\beta = \beta_0 + \beta_1 * \log(Wc) + \beta_2 * V_5 + \beta_3 * V_1 + \beta_4 * (Wc9 * V_4)$;

V_i denotes i^{th} clone, BL_3 = block 3 and Wc = weeding treatments,

log = natural logarithm, T = age.

The function Log(Wc) described the relationship between weed free area/tree on the coefficient values better than linear or quadratic functions (see section 4.4.4).

A summary of the coefficient values is given in the following table.

Table 4.1: Table for the alpha coefficient for mean height model

Coefficient	Name or Dummy variable	Estimated value
α_0	default	0.214145
α_1	Log(Wc = weed free area/tree)	0.007240
α_2	clone 2	-0.014313
α_3	clone 4	0.021572
α_4	Wc9*Clone 4 interaction	-0.014456
α_5	Block 3	0.0146865

Table 4.2: Table for the beta coefficient for mean height model

Coefficient	Name or Dummy variable	Estimated value
β_0	default	1.736817
β_1	Log(Wc = weed free area/tree)	0.185385
β_2	clone 5	-0.182686
β_3	clone 1	-0.095953
β_4	Wc9*Clone 4 interaction	-0.068371

The variation in alpha and beta with increasing weed free area per tree was modelled using a logarithmic function; $\alpha, \beta = \delta + \gamma * \log(Wc)$ (4.19). The model outputs obtained using this approach were similar to those obtained by using dummy variables for treatments that differed significantly in α and β (Table 4.3 below).

Table 4.3: Model outputs for mean height using normal dummy variables and log(Wc).

Model	Residual MSE	Mean	Skewness	Kurtosis	Range of residuals
Log function	0.00579773	-0.00006	-0.32831	1.789049	-0.26772 to +0.252935
Normal dummys	0.00617058	-0.00027	-0.09992	1.818385	-0.26652 to +0.283528

The model predicted mean height to within ±0.28 m (-27 to +25 cm) of the measured values. Plots of residuals versus predicted and all independent variables showed normal distributions with little evidence of bias (Figures 4.1 - 4.6). In all cases, different colours show weeding treatments or clones (see legend).

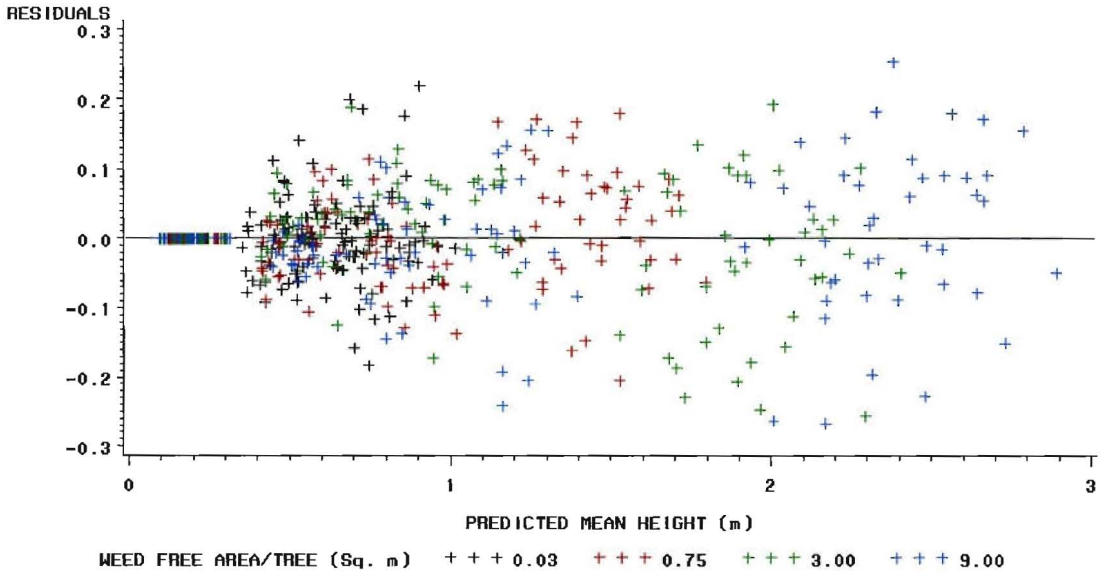

Figure 4.1: Plot of residuals versus predicted mean height (m).

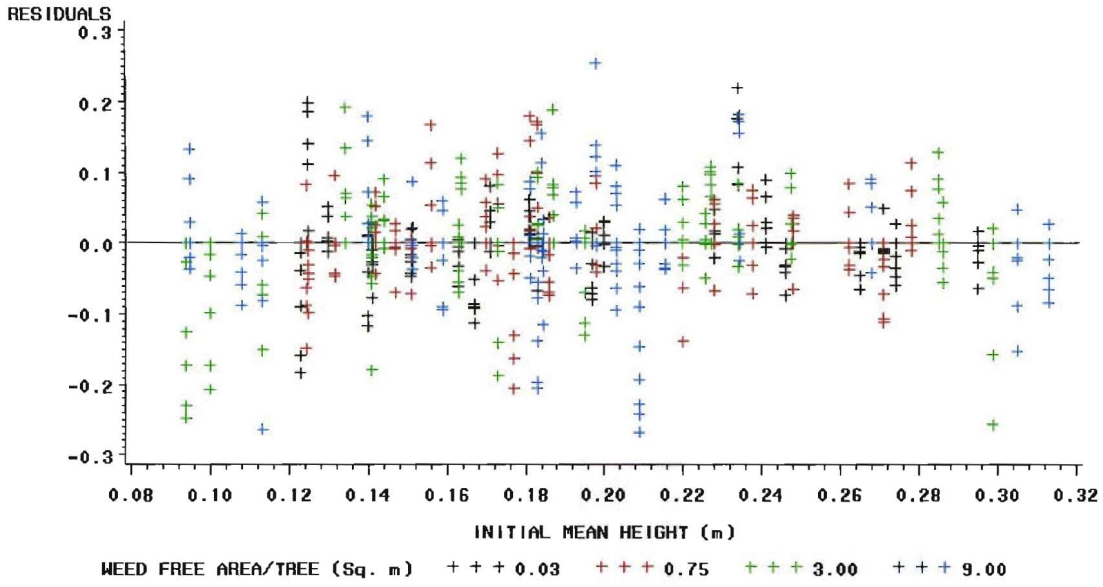

Figure 4.2: Plot of residuals versus initial mean height measured at age = 0.

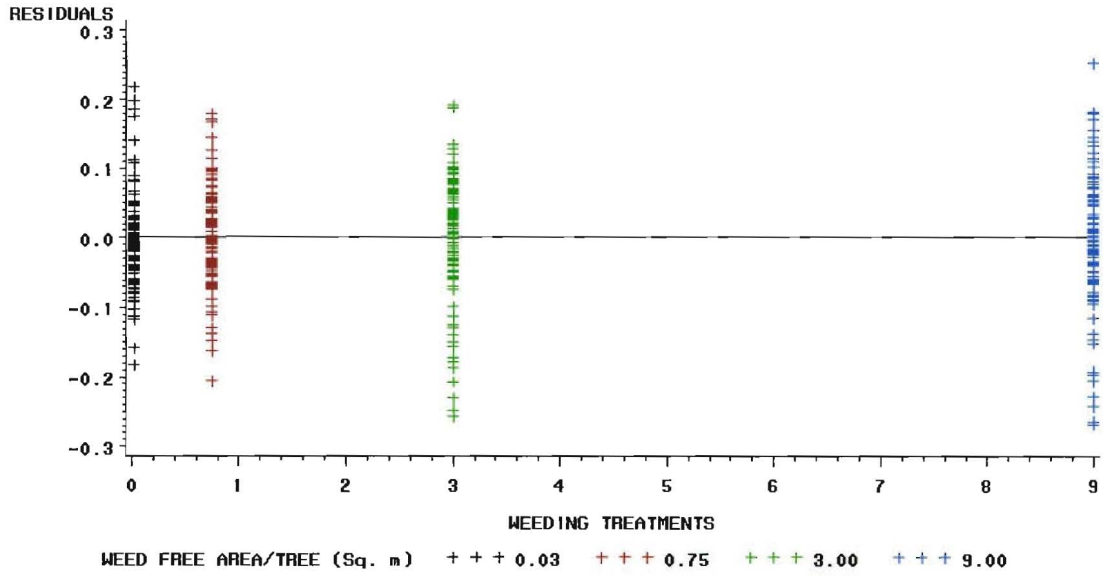

Figure 4.3: Plot of residuals versus weeding treatments for mean height (m).

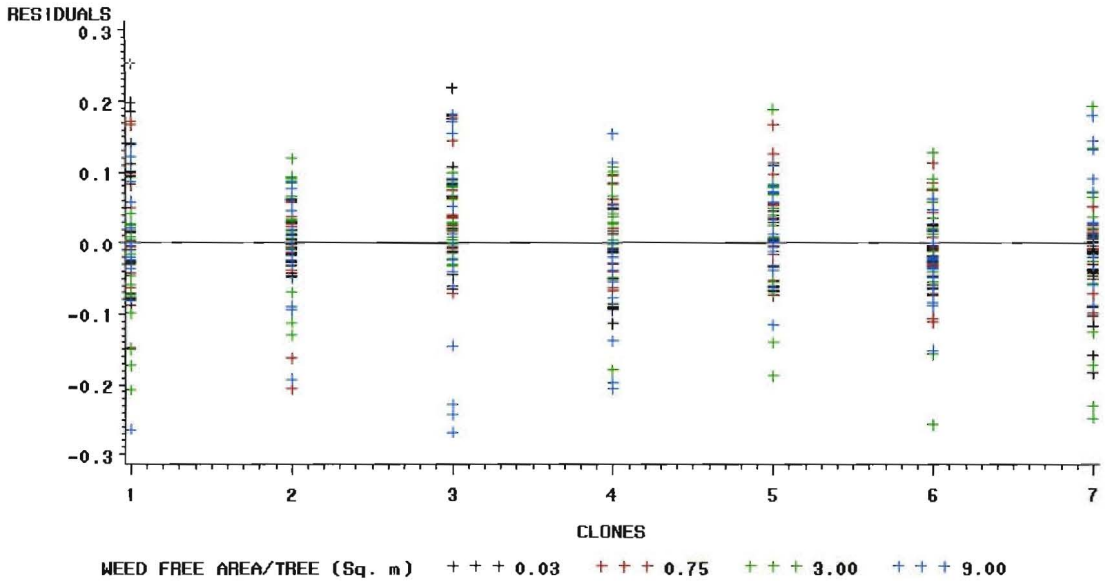

Figure 4.4: Plot of residuals versus clones for mean height (m).

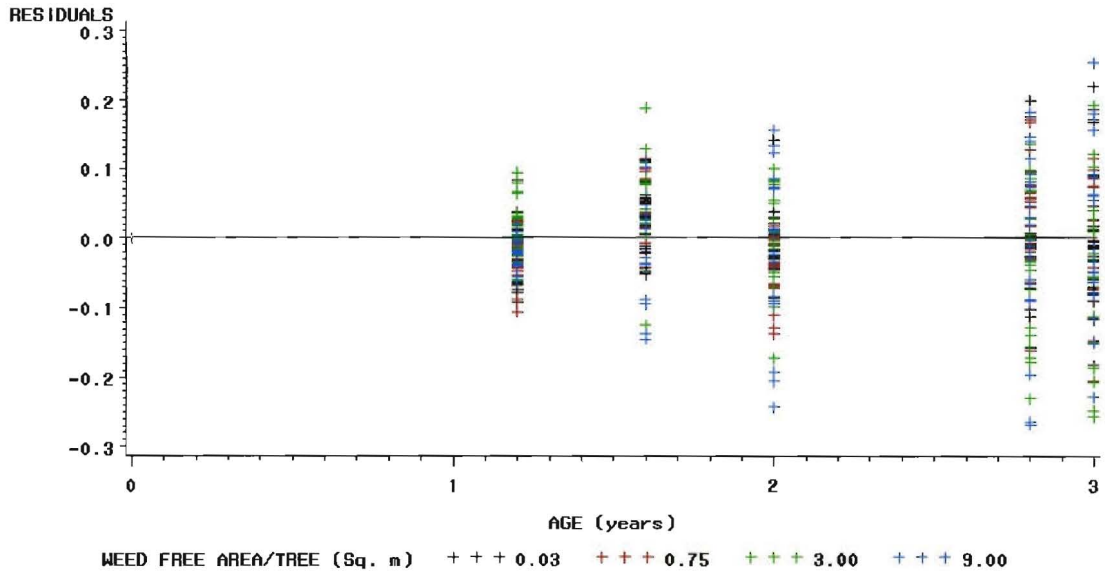

Figure 4.5: Plot of residuals versus tree age for mean height (m).

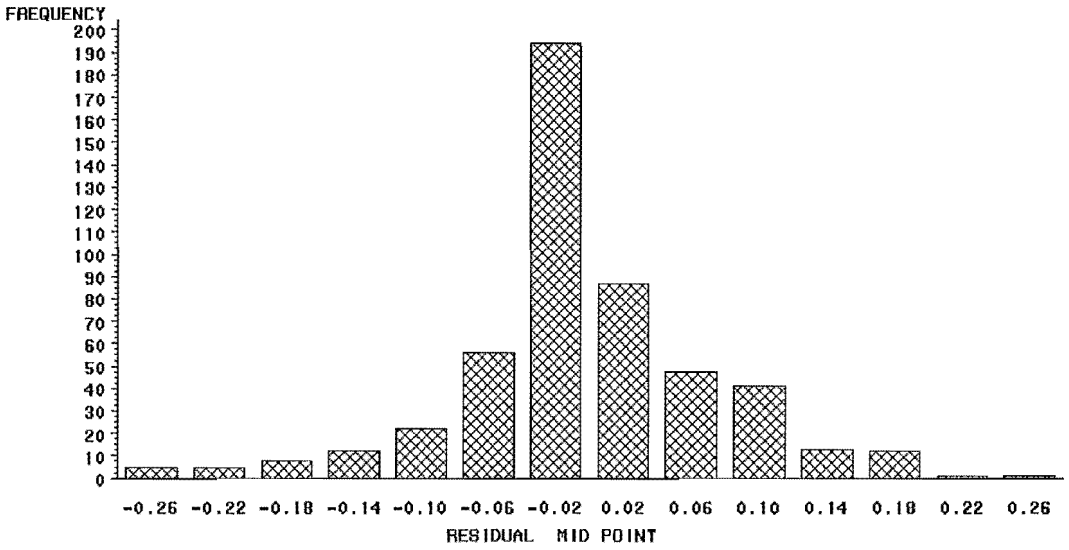

Figure 4.6: Frequency distribution of residuals for mean height model.

4.4.2 Basal-basal area per hectare models

The final model for basal-basal area per hectare was equation 4.17;

$$G_{GLT} = G_{GLT=0} + \alpha * N_{T=0} * T^{\beta};$$

$\alpha = \alpha_0 + \alpha_1 * V_{1,2,5} + \alpha_2 * V_7 + \alpha_3 * (BL_3 * Wc9) + \alpha_4 * Wc9;$

$\beta = \beta_0 + \beta_1 * \log(Wc);$

V_i denotes i^{th} clone, BL_3 = block 3 and Wc = weeding treatment,

log = natural logarithm and T = tree age.

A summary of the coefficient values is given in the following table.

Table 4.4: Table for the alpha and beta coefficients for basal-basal area model.

Coefficient	Name or Dummy variable	Estimated value
α_0	default	0.008237
α_1	clones 1, 2 and 5	-0.0018742
α_2	clone 7	-0.0008256
α_3	Block 3*Wc9 interaction	0.00112982
α_4	complete weeding, Wc9	0.0006923
β_0	default	2.807137
β_1	Log (Wc = weed free area/tree)	0.3920187

The variation in beta with increasing weed free area per tree was modelled using a logarithmic function (equation 4.19); $\beta = \delta + \gamma * \log(Wc)$ and was included as a linear term of the basal-basal area/ha model. The model predicted mean basal-basal area to within ±63 cm^2 (-62.9 to +58.3) of the observed values. Plots of residuals versus predicted and all independent variables showed normal distributions with no apparent bias (Figures 4.7 - 4.12), different colours are as described earlier.

Table 4.5: Model outputs for basal-basal area per hectare model.

Basal-basal area (cm^2)	Residual MSE	Mean	Skewness	Kurtosis	Range of residuals
model outputs	187.5226	-0.06634	-0.14152	4.27336	-62.8533 to +58.3258

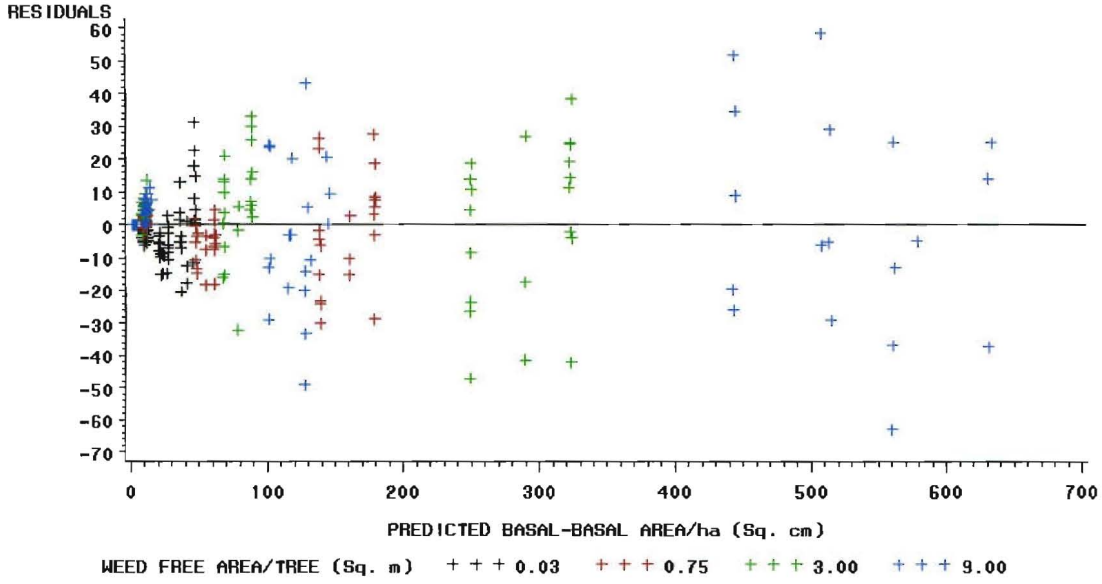

Figure 4.7: Plot of residuals by predicted for basal-basal area (cm^2) per hectare.

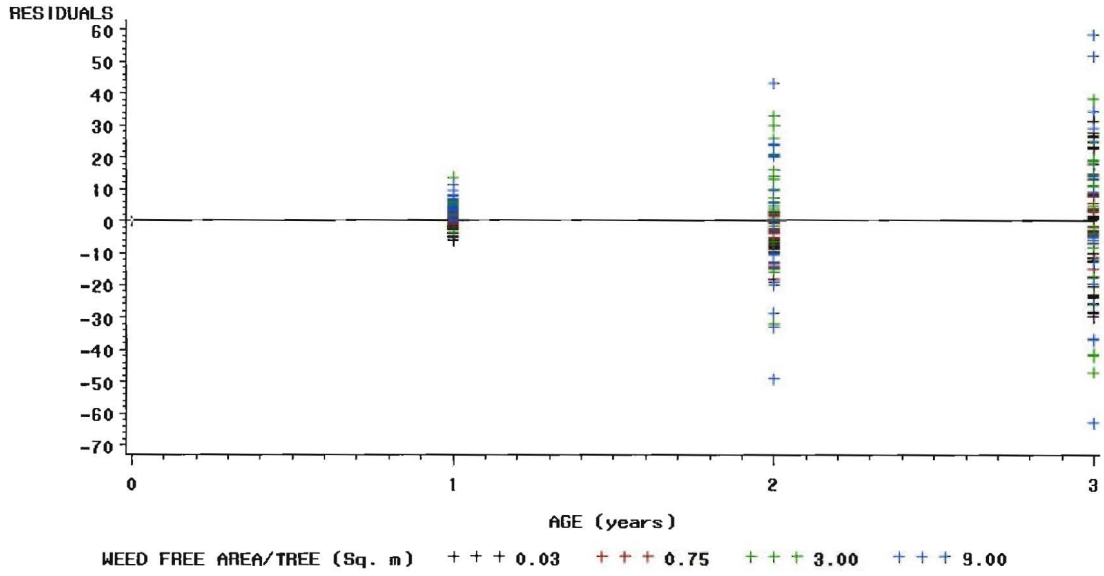

Figure 4.8: Plot of residuals by age for basal-basal area (cm^2) per hectare.

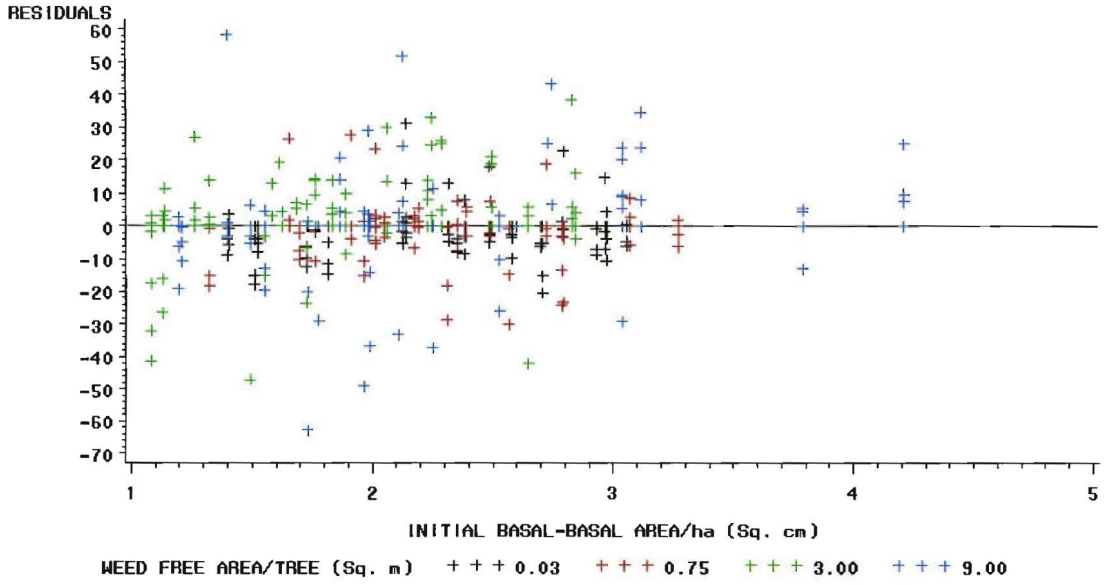

Figure 4.9: Plot of residuals by basal-basal area (cm^2) per hectare at planting.

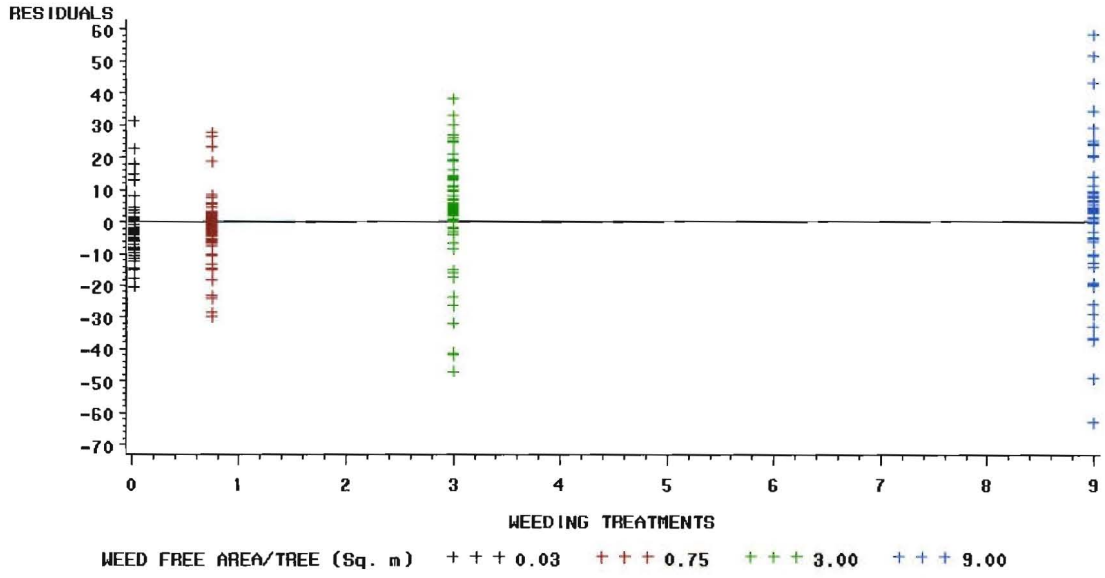

Figure 4.10: Plot of residuals by weeding treatments for basal-basal area (cm^2) per hectare.

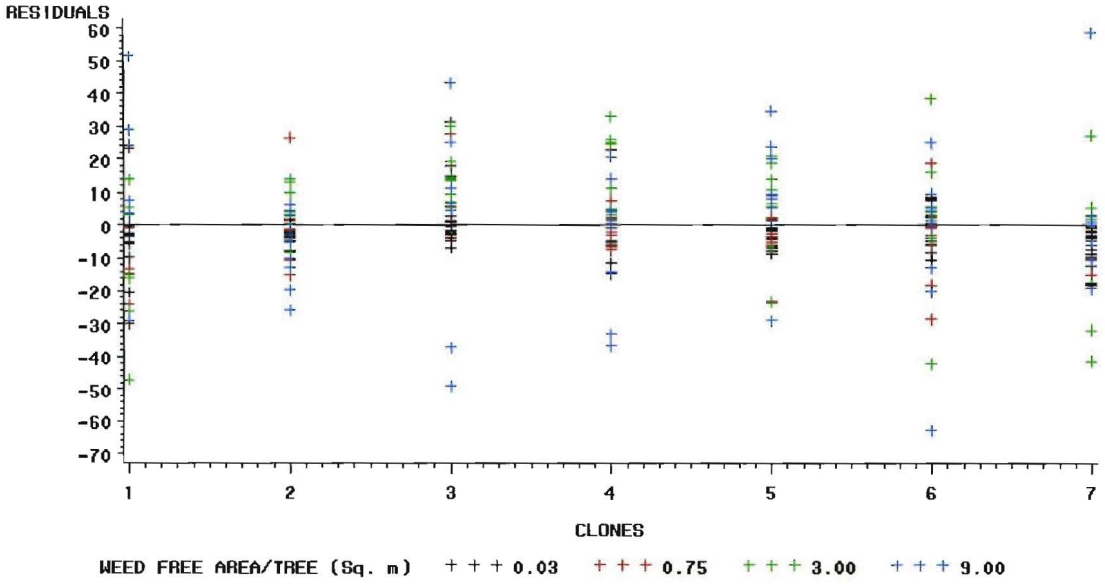

Figure 4.11: Plot of residuals by clones for basal-basal area (cm^2) per hectare.

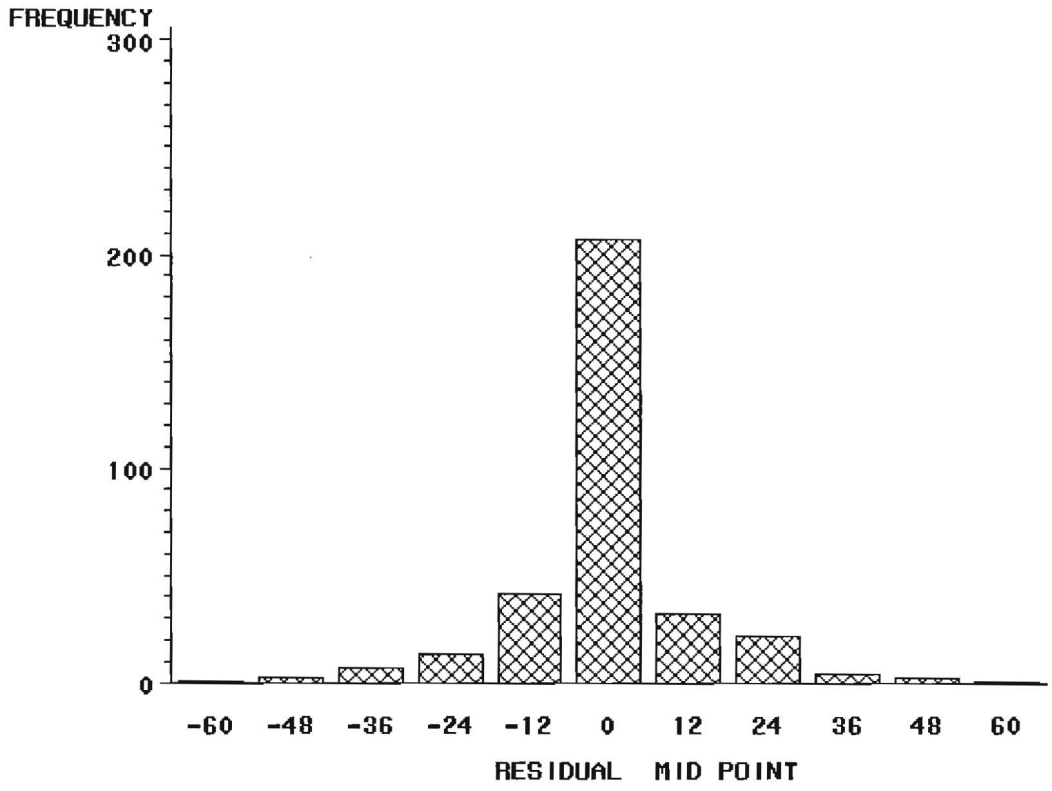

Figure 4.12: Frequency distribution of residuals for basal-basal area per hectare model.

4.4.3 Survival models

In modelling tree survival per hectare, the following models were tried;

1) $N_2 = N_1 \exp\left(-\alpha\left(T_2^{\beta} - T_1^{\beta}\right)\right)$ (4.20)

2) $N_2 = N_1^{\left(\frac{T_2+1}{T_1+1}\right)}$ (4.21)

3) $N_2 = N_1\left(\frac{T_1+1}{T_2+1}\right)\alpha * \exp\left(-\alpha\left(T_2^{\beta} - T_1^{\beta}\right)\right)$ (4.22)

4) $N_2 = N_1 \exp\left(\beta(T_2 - T_1) + \alpha\left(1 - \exp\left(\beta(T_2 - T_1)\right)\right)\right)$ (4.23)

5) $N_2 = N_1\left(N_1^{-\beta} + \alpha\left(T_2^{\gamma} - T_1^{\gamma}\right)\right)^{-1/\beta}$ (4.24)

Equations 4.20, 4.21 and 4.22 are anamorphic while equations 4.23 and 4.24 are polymorphic in form. Anamorphic equations are a family of curves allowing for differences in asymptotes but maintaining the same general shape. On the other hand polymorphic equations allow for changes in shape while maintaining the same asymptote.

The difference equation; $N_2 = N_1 \exp\left(-\alpha\left(T_2^{\beta} - T_1^{\beta}\right)\right)$ (4.20), was found to best describe stems per hectare survival. This equation in yield form is

$$N_T = \exp\left(\alpha * T^{\beta}\right) \quad (4.25)$$

The parameter values were $\alpha = 0.12382+0.4225*M_1+0.114872*M_2$ and $\beta = 1.41832$. M_1 was a dummy variable for clone 1 growing in Wc9 while M_2 was a dummy variable for clones 1 and 2 growing in Wc0.03.

Table 4.6: Model outputs for survival per hectare model.

Stem Survival/ha	Residual MSE	Mean	Skewness	Kurtosis	Range of residuals
model outputs	19766.203	-0.58725	-1.15316	2.6655	-523 to +255

Results of the logistic model, $p = \frac{1}{1+\exp(-k)}$ (4.26) (Woollons 1998),

where $k = \alpha_0 + \alpha_1 X_1 + \alpha_2 X_2 + ... + \alpha_n X_n$ (4.27),

X_1 to X_n are independent variables and α_0 to α_n are coefficients, were;

$$k = -0.9213 + 1.8103 * Wc0.03 + 1.1183 * Clone1 + 1.1183 * Clone3 - 0.9213 * T_I - 1.4213 * Clone4 \quad (4.28).$$

Results of the logistic equation showed that clones 1 and 3 were positively related to mortality and so was the control, Wc0.03. Meanwhile, less tree death is expected with age and in clone 4. Residual plots for the survival model are shown in figures 4.13-4.18.

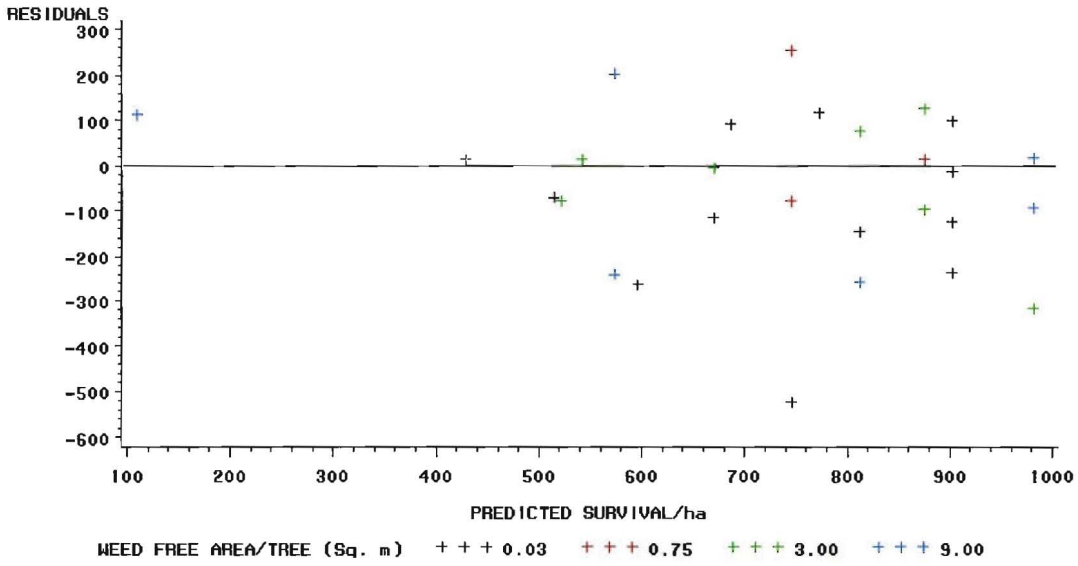

Figure 4.13: Plot of residuals versus predicted stems/ha survival.

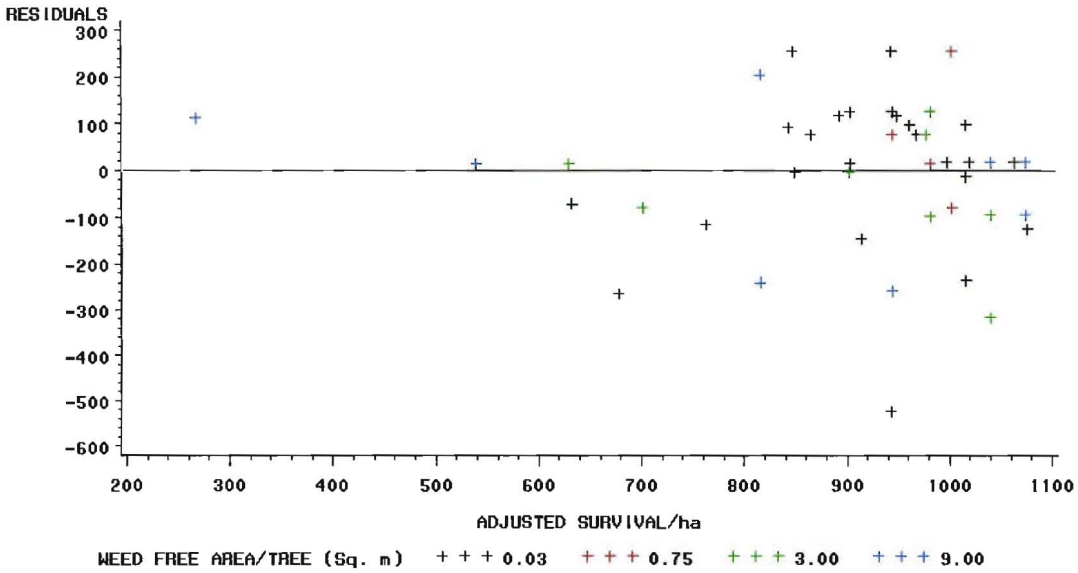

Figure 4.14: Plot of residuals versus predicted stems per hectare survival after adjusting for probability of mortality.

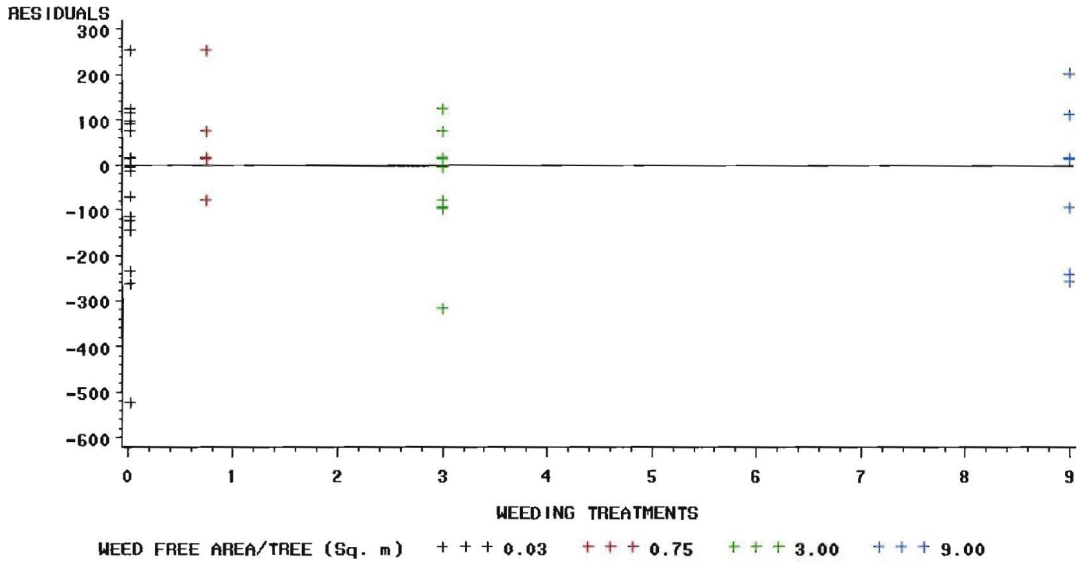

Figure 4.15: Plot of residuals versus weeding treatments for stems per hectare survival.

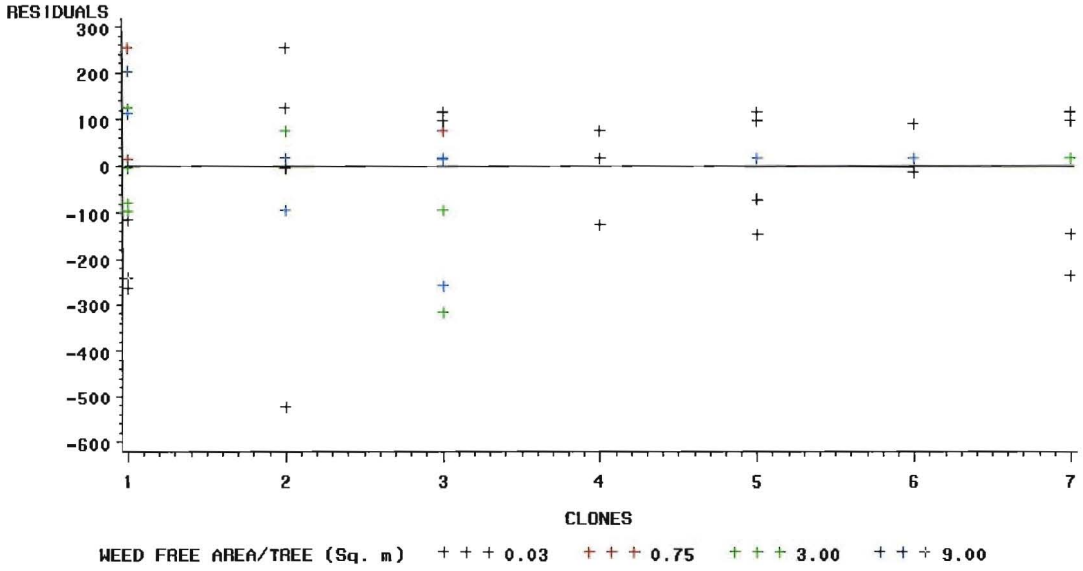

Figure 4.16: Plot of residuals versus clones for stems/ha survival model.

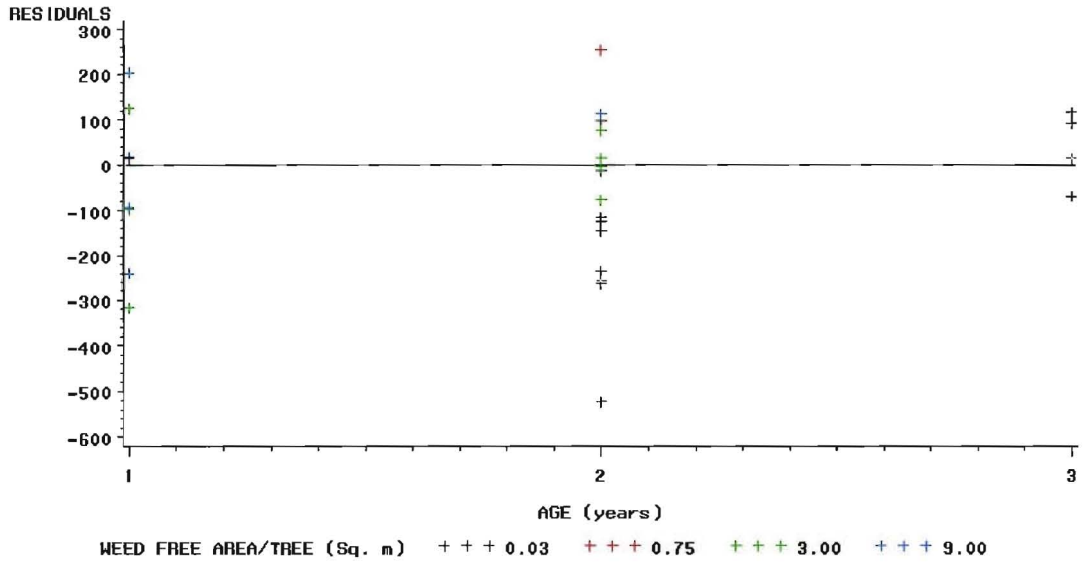

Figure 4.17: Plot of residuals versus tree age for stems/ha survival model.

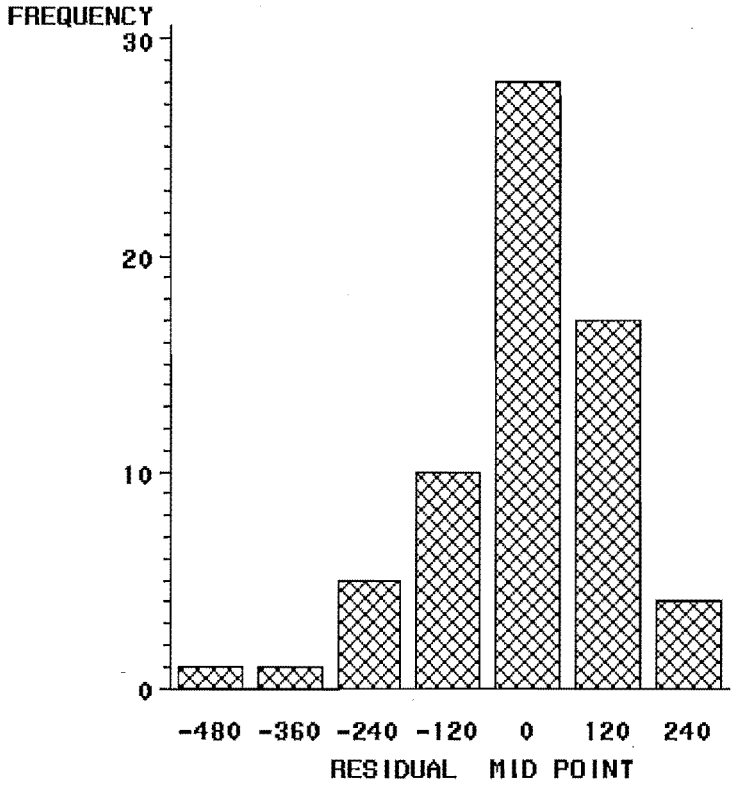

Figure 4.18: Frequency distribution of residuals for survival/ha model.

4.4.4 Parameter analysis for mean height and basal-basal area models

Competition from weeds affected both α and β parameters of the models. Both α and β increased sharply with increasing weed free area per tree in moving from the control to 0.75 m^2 spots and thereafter gradually to a maximum at 9 m^2 spots (Figure 4.19).

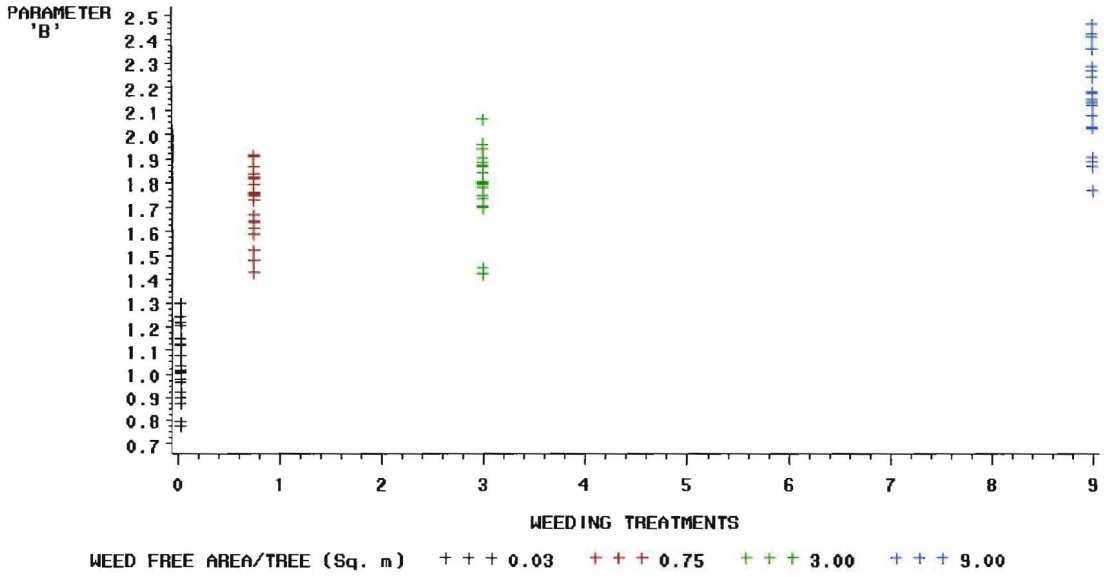

Figure 4.19: Relationship of the β coefficient by weed free area per tree.

For mean height, alpha (rate coefficient) differed significantly between Wc9 and Wc3 both of which differed significantly from Wc0.75 and Wc0.03. No significant differences were observed between Wc0.75 and Wc0.03 for alpha. For beta (shape coefficient), Wc9 and Wc0.03 differed significantly from each other and from the other two weeding treatments. Wc3 and Wc0.75 were not significantly different from each other.

For basal-basal area the alpha coefficient did not differ significantly between Wc9 and Wc3 nor between Wc0.75 and Wc0.03 but both groups differed significantly from each other. For the beta coefficient all weeding treatments were significantly different from each other. Clone 1 differed significantly from clones 3, 4, 5 and 6 while clone 3 differed significantly from clones 2, 7 and 1 for alpha. For beta, clone 5 differed significantly from clones 7, 2 and 1. No significant differences were observed amongst the other clones. Some significant blocking effects were also observed. Block 3 was significantly different from block 1 and 2 for alpha in mean height (Table 4.1). There was a significant interaction between clone 4 and Wc9 for α and β for mean height (Tables 4.1 and 4.2).

4.5 DISCUSSION

4.5.1 Height and basal-basal area

Weeding increased tree height and diameter growth in agreement with findings by other researchers (Mason 1992, Richardson 1993, Mason *et al.* 1996b, Mason and Whyte 1997, Zhao 1999, Mason and Kirongo 1999). The presence of weeds (Wc0.03) reduced the rate and curvature of the growth curves leading to more-or-less straight trends (Figure 4.20). By the end of the third growing season trees growing in plots with some form of weed control were more than twice the height of those growing in unweeded plots (Figure 4.20). Similar trends were observed for basal-basal area per hectare with time (Figure 4.21).

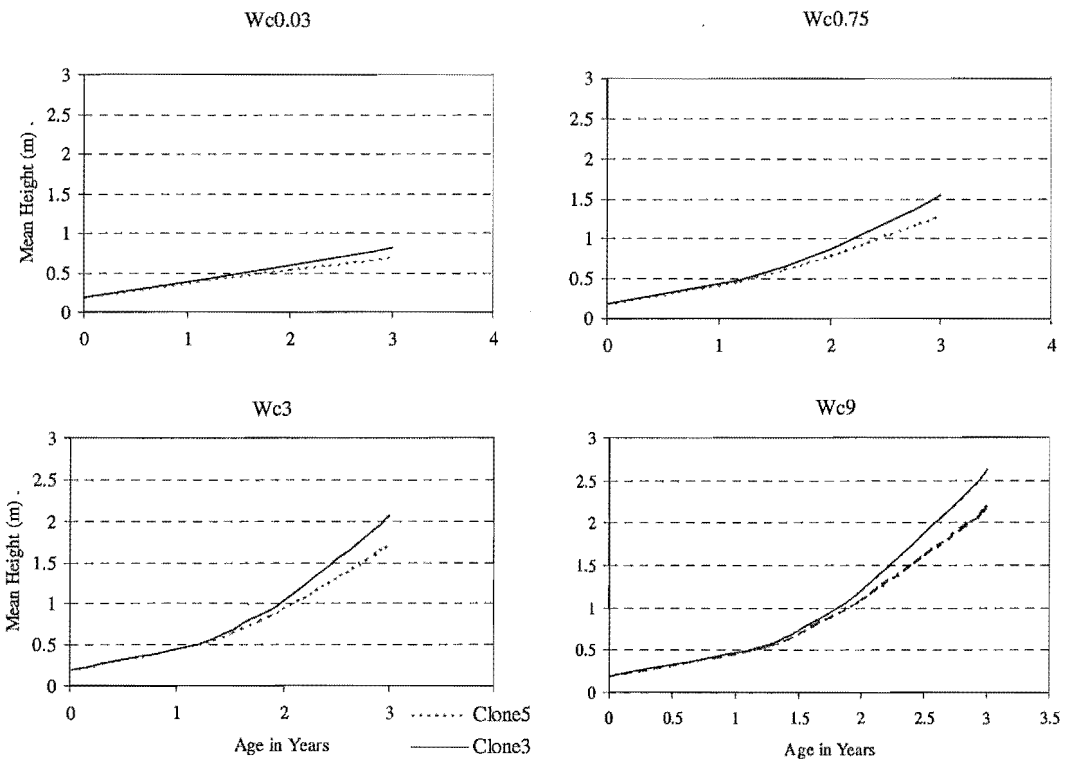

Figure 4.20: Mean height (m) of clones 5 and 3 during the 3 year study period for trees in the control (Wc0.03), 1 m spots (Wc0.75), 2 m spots (Wc3) and complete weeding (Wc9). Clones 3 and 5 had significantly different β coefficients.

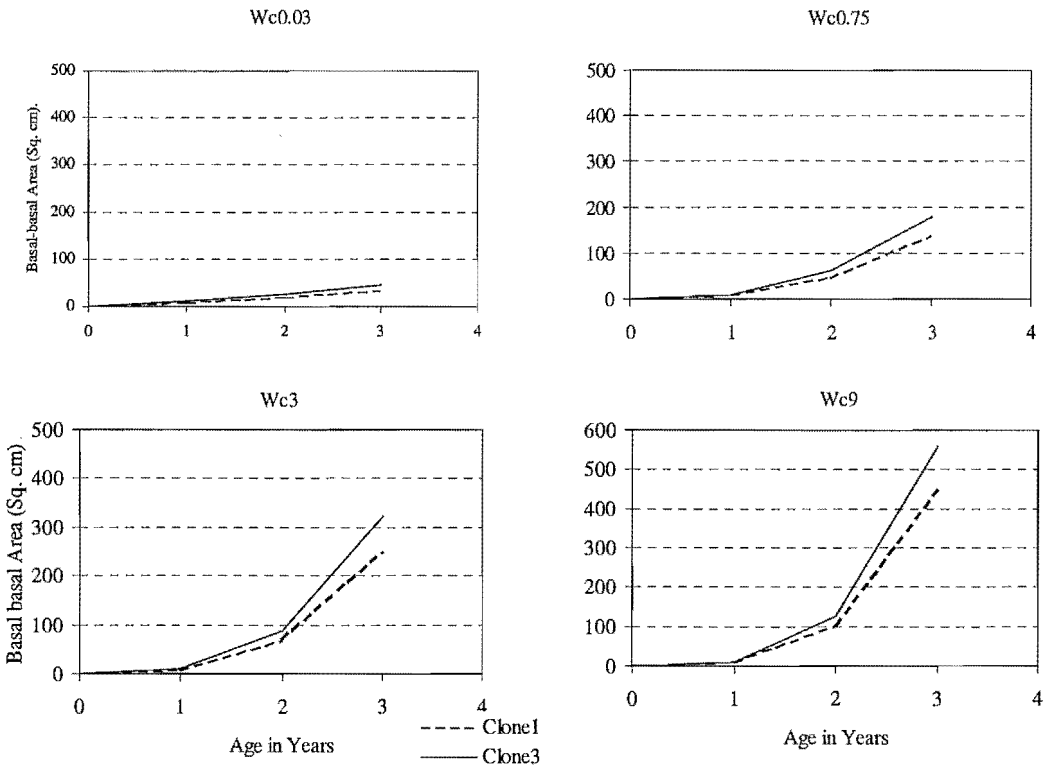

Figure 4.21: Basal-basal area (cm^2)/ha of clone 1 and 3 during the 3 year study period for trees in the control (Wc0.03), 1 m spots (Wc0.75), 2 m spots (Wc3) and complete weeding (Wc9). Clones 1 and 3 had significantly different α coefficients.

The effect of genotype was also vivid with some clones showing better growth than others in all the four growing environments (Figures 4.20 and 4.21 - the chosen clones displayed significantly different ($\alpha = 0.05$) rate and/or shape parameters). Mason and Kirongo (1999) postulated a hypothetical scenario showing how clonal effects may be expressed. In this study it is quite evident that such clonal differences do exist even at this early age. Whether these differences will be maintained or not will depend on a number of factors, for example the weather patterns (drought) and internal (tree) factors which influence growth. For example clone 3 had higher leaf areas than clone 1 and this offered some advantage during the third growing season. However, this advantage may be reduced if the increased foliage results in significant self-shading leading to decreased carbon-fixation potential, an aspect which needs investigating further. Thus while clone 3 is doing very well, continued observations

will be worthwhile in the future. Moreover, some clonal effects could be related to difficulty with establishment rather than growth potential once established.

4.5.2 Tree survival

The control of unwanted vegetation increased tree growth and reduced tree mortality. The logistic procedure showed that trees growing with weeds had a higher probability of dying than those in weeded environments. Meanwhile different clones displayed variations in mortality, with clone 1 and 3 showing a high probability of dying and clone 4 showing a negative correlation.

These findings are in agreement with those reported by others. For example, West (1984), Wagner *et al.* (1989), Mason (1992), Evans (1992), Richardson (1993), Richardson *et al.* (1996b) (at one site) and Mason *et al.* 1996b (at a higher altitude site) found weeding to increase tree survival. The reported differences between some clones imply that some genotypes are more resilient than others. Many trees died shortly after planting and during the prolonged drought in the second growing season, particularly in the weedy plots. This suggests that the initial deaths were due to transplant stress as reported earlier by Mason and Kirongo (1999) as well as due to water stress later during the second growing season.

Modelling mortality using the two-stage procedure as suggested by Woollons (1998) made use of all the data and resulted in slightly better looking residuals. However, the data set was poor in that only a total of 252 observations were available. Thus the improvement was not immense.

4.5.3 Duration of weed control treatment effects

Weed control treatment effects were still evident in all weeded treatments at the end of three years. Trees in the complete weeding treatment showed a strong upward

(diverging) trend to all the other treatments (type II). While both the 2 m and 1 m spot treatments showed increasing divergence compared to the unweeded control (type II), the trends between them were more or less parallel (type I) (Figure 4.22). Similar trends were found for GLD. Thus by the end of year 3 (from this data) the advantages of having 2 m spot diameters as opposed to 1 m spot diameters had started to wear off.

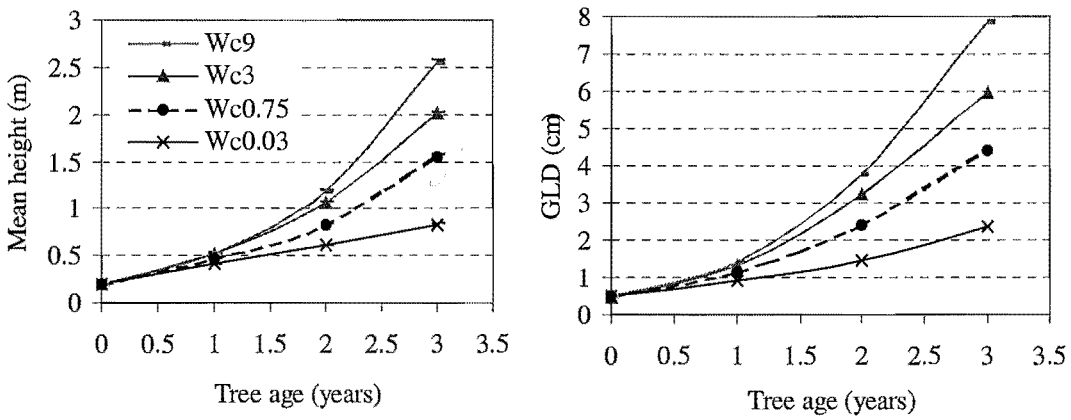

Figure 4.22: Mean height (m) and GLD (cm) vs age for weeding treatments.

The managerial implications of these results are profound. For one, these results show that weeding offered some advantages resulting in higher tree growth and survival. The duration of the spot weed control treatment effects (2 m vs 1 m) had started to wear off by the end of the third year. This may imply that if the differential weed competition effects were removed and all plots were completely weeded, trees of the same size but from different treatments would not immediately grow in similar fashion. However, it can be postulated that after a period of adjustment there would be a gradual trend towards a parallel growth trajectory (i.e. type I). There may also be weed competition for resources at levels that vary among treatments as well. However, this may not necessarily continue indefinitely and continued observations are needed.

However, perhaps the most significant is the observation that genotypic effects were already vivid after only 3 years in the field resulting in significant growth

differences. This is contrary to common belief (e.g. Burdon 1995) that advantages of clonal treatments were significant only after the juvenile phase. Mead *et al.* (1993) reported significant differences in toppling (a lean of more than 15 degrees from the vertical position) frequency with the fastest growing clone showing lowest frequency. It was evident in this study that clones 1 and 5 were less suited to the site and forest managers in Dunsandel would not benefit much from their use. However, forest managers may need to wait longer before embracing clones with massive foliage and fast growth (e.g. clone 3) as these may easily fall prey to the Nor'westerlies which are notorious in the Canterbury plains. Continued observations need to be taken until rotation age.

4.6 CONCLUSIONS

1. Weeding increased tree height and diameter growth and improved survival.
2. The presence of weeds reduced the rate and curvature of the growth curves.
3. By the end of the third growing season trees in the control were less than half the size of those in weeded plots representing time gains of more than 1 year.
4. The advantages of having 2 m diameter spots as opposed to 1 m diameter spots had started to diminish.
5. Different clones displayed differences in growth and survival an advantage which may benefit forest managers in Dunsandel.
6. The logistic procedure showed that trees growing with weeds had a higher probability of dying than those in weeded environments.
7. Forest managers need to site match clones to reap maximum benefits from the use of clones.

CHAPTER 5

CROWN FOLIAGE BUDGETS AND GROWTH DYNAMICS

PREAMBLE

Detailed morphological and physiological measures of plants are essential if we wish to better understand the way tree crops modify their growth processes in response to changes in the environment. Models of tree growth that use changes in plant processes have the potential to be applicable to a broad range of sites and growing conditions (Landsberg 1986, Adlard 1995) while at the same time showing the necessary dynamics in growth processes in a better way than conventional measures e.g. diameter (Beets and Whitehead 1996). Detailed measures can be time consuming and costly, however. One way of alleviating this problem is to use non-destructive measures of crown size and relate these to tree biomass or foliage dry weight using regressions developed from a small representative sample.

One such surrogate measure used in this study was tree crown areas on photographs. Limited destructive sampling was used to develop relationships between crown areas on photographs to tree biomass and foliage dry weight. The resultant equations were used to estimate standing tree biomass and leaf weight. The biomass estimates from crown photo area models showed very good concordance to actual total tree biomass from the summation of stem, branches and foliage portions measured on some destructively sampled trees in Wc0.75 weeding treatment.

Models of crown foliage budgets have two main inputs, 1) leaf area additions and 2) leaf area losses; both of which can be expressed as functions of space and time. Specific information relating to foliage growth dynamics, leaf area spatial distribution and above ground partitioning was needed to enable reliable estimates of

leaf area additions. Leaf area losses on the other hand were quantified from actual needle survival counts from needle mortality sampling units located in various positions in the crown.

To make this chapter comprehensible, it was divided into 2 complementary parts. Part 1 discusses studies which enabled estimation of leaf area additions while part 2 is dedicated to quantification of leaf area losses. Each part has a brief introduction, detailed methodology, results and a brief discussion. At the end of the chapter is a synthesis which puts the results of the 2 parts into perspective.

PART 1: LEAF AREA ADDITIONS

5.1 INTRODUCTION

Tree crowns are vital as they harbour foliage; the sites where most physiological processes important for growth, for example light interception, photosynthesis and respiration take place (Baker *et al.* 1984, Beets and Lane 1987). Leaves are the productive investment of the tree and untimely loss by defoliation or hampered development due to stress (e.g. water stress) can lead to severe basal area and volume growth losses in radiata pine (Rook and Whyte 1976, Benson *et al.* 1992). Tree crowns can also indicate water use potential (Linder *et al.* 1987, Pook 1984). Large crowns carry more foliage but can also transpire excessively during drought causing stress.

Previous studies have shown that crown structure variables are useful determinants of tree growth (Dalla-Tea and Jokela 1991, Linder *et al.* 1987, Borghetti *et al.* 1986). For example, Carbon-fixation has been related to the amount, temporal and spatial distribution of foliage (Kinerson *et al.* 1974, Grace *et al.* 1987b, Hunter *et al.* 1987) and light interception and use efficiency (Grace *et al.* 1987a, Leverenz *et al.* 1982, Beadle *et al.* 1985, Wang and Jarvis 1990, Landsberg 1986).

Tree crowns are heterogeneous, however. Crown structure variables, e.g. shape (geometric form, Xu (2000)), branch architecture and morphology can vary significantly even for two seemingly 'similar' canopies. Light penetrability, water vapour levels, temperatures, CO_2 levels and leaf ventilation are all dynamic characteristics. Leaf area density significantly influences light attenuation patterns within crowns. Different crown parts differ in their leaf area spatial distribution as well. All these factors influence the rate of photosynthesis and the gross amount of carbon fixed (Landsberg 1986, Kinerson *et al.* 1974, Grace *et al.* 1987b, Beadle *et al.* 1985, Leverenz *et al.* 1982, Beets 1977, Watts *et al.* 1976, Wang and Jarvis 1990).

One of the important foliage measures in a tree is specific leaf area (SLA). It is the ratio between leaf area and leaf dry weight (Causton and Venus 1981). Growth rates of new foliage and the ratio of this new foliage to that already on the tree can have significant influences on SLA and C-fixation capacity (Watts *et al.* 1976, Shelton and Switzer 1984). New fully expanded foliage is the most efficient in PAR use and hence C-fixation (Woodman 1971, Watts *et al.* 1976, Leverenz *et al.* 1982, Xu 2000). High growth rates of new foliage can therefore lead to increased absorption of usable light (PAR) and C-fixation (Beadle *et al.* 1985, Dalla-Tea and Jokela 1991).

While studying the influence of crown structural properties on PAR absorption and photosynthesis in Sitka spruce, Wang and Jarvis (1990) reported total area of foliage and its spatial distribution to be the primary factors influencing radiation absorption and use. Implicit in this statement, however is the fact that total production depends not only on total foliage amounts but also on the following;

1) proportions of the various age classes present (current foliage is known to be more efficient in PAR absorption and use than older foliage (Wang and Jarvis 1990, Woodman 1971, Watts *et al.* 1976, Leverenz *et al.* 1982, Xu 2000)). Trees with more young foliage are physiologically better able to grow (Menzies *et al.* 1991).
2) functional leaf area in each age class, for example trees growing under moisture stress tend to have chlorotic foliage and therefore, reduced 'useful' leaf area (Kirongo and Mason 1999, Zutter *et al.* 1986).
3) growth rate and development of current foliage - high expansion rates and unchecked development lead to fully expanded fascicles with maximum leaf area (Rook and Whyte 1976) and therefore increased PAR absorption and C-fixation (Beadle *et al.* 1985, Dalla-Tea and Jokela 1991).
4) physiological state of the foliage, for example water stress (due to competition from weeds) (Landsberg 1986) may reduce foliage efficiency.

Important also in determining gross production and tree growth is the canopy leaf area balance. This is defined as the sum of new foliage and the net amounts remaining from previous seasons after adjusting for fascicle mortality due to biotic

and abiotic causes (Pook 1984, Landsberg 1986). Trees that shed most of their older foliage and replace it with new more efficient foliage are better able to grow rapidly. This aspect of crown studies will be discussed in part 2 of this chapter.

Models of canopy production, therefore need to have accurate estimates of leaf area growth dynamics, both in space and time and estimates of losses of functional leaf area (death or senescence) or reduction (browsing, defoliation, chlorosis). Three factors are seen to be important in canopy production models:

1) allocation patterns to 'wood' and foliage with time; hence
2) temporal estimates of leaf area production; and
3) needle mortality patterns in space and time by needle age classes.

From these measures an equation denoting canopy production can be formulated;

$$LACanopy = \Delta fol_1 + \sum_{i=1}^{n} (Totfol_i - Lostfol_i) \qquad (5.1)$$

where;

LACanopy = canopy leaf area balance;

Δfol $_1$ = current season's leaf area;

Totfol $_i$ = leaf area of age i; where i is greater or equal to 2;

Lostfol$_i$ = lost leaf area of age i (senescence, browsing, defoliation); and

n = foliage age class.

In order to quantify the canopy leaf area balance and develop a functional crown foliage budget model, a number of input variables were required. Specific studies were carried out to quantify these aspects as itemised below.

1) Foliage growth dynamics including leaf area spatial and temporal distribution were studied. These variables were useful to capture the dynamics of PAR interception (and possible use) in different crown parts. Soil moisture availability during the third growing season was measured and related to needle growth during the same period.

2) Crown structure representation (e.g. branch sizes, branch order and whorls) together with above ground biomass allocation patterns to stem, branches and foliage components were studied. The proportion of foliage in the stem and branches were especially useful in quantifying overall foliage losses from the tree. Meanwhile, crown structure measures were important input variables in needle mortality studies (4 below).

3) Quantification of total tree leaf area amount by tree age. Image analysis techniques combined with limited destructive sampling were useful in this regard. Relationships between crown photo area and total tree biomass and leaf dry weight were developed. The relationships were applied to data from 'standing' trees of the same clones with crown photo area of standing trees as the dependent variable. Information from leaf area growth dynamics (1 above) was used to develop regressions of leaf area vs. leaf weight. The regressions were used to estimate standing tree total leaf area.

4) Needle mortality was quantified by actual counting of live and dead needle fascicles in sampling units set up in the crowns of selected trees. Mortality of needles was related to needle age, tree age, tree size (included structure variables from 2 above), crown position, weeding and clonal treatments. The needle mortality data was used to estimate leaf area losses, the subject of part 2 of this chapter.

All the detailed studies were carried out on only 3 out of the 7 available clones. These were clone 1 (slowest growing at the end of the first year), clone 2 (intermediate in growth rate) and clone 3 (fastest growing). Limited destructive sampling was carried out on trees set aside for the purpose at the beginning of the experiment.

5.1.1 Importance of crown dynamics studies

Many researchers have reported decreased tree height and diameter growth as a result of increased weed infestation on a site (Richardson 1993, Wagner and Radosevich 1991a, Nambiar and Sands 1993, Nambiar and Zed 1980, Kirongo 1996, Mason and Kirongo 1999). Reduced tree growth has been related to moisture stress (Nambiar and Zed 1980, Sands and Nambiar 1984, Benson *et al.* 1992, Nambiar and Sands 1993), nutrient (Linder *et al.* 1987, Smethurst and Nambiar 1989, Snowdon and Benson 1992, Benson *et al.* 1992) and reduced leaf surface area (Shelton and Switzer 1984, Zutter *et al.* 1986, Zutter *et al.* 1999a) in many instances. Genetics and the interaction between genotype and the environment have been reported to result in growth differences (Theodorou *et al.* 1991, Madgwick 1994, Bollmann and Sweet 1976, 1979, Bollmann *et al.* 1986).

The effects of varying competition intensity on different genotypes as regards foliage emergence, development and distribution in the crown are not well known, however, especially for juvenile radiata pine. Most studies have dwelt on crops older than age 5 or species other than radiata pine or those growing in sites where water is not limiting. There is a need, therefore, for modelling of leaf age profiles including production and losses, and leaf area distribution within canopies of juvenile radiata pine. Models should represent how these variables are influenced by crown position, time, fascicle age, cultural treatments (e.g. weeding) and/or genotype.

The aims of the studies described in this chapter were to partially explain how the growth differences in height and GLD reported in Chapter 4 may have arisen. The following sub-sections highlight the main methodologies used in collecting data.

5.2 METHODS

5.2.1 Foliage growth dynamics and leaf area spatial distribution

The objective of this study was to quantify needle elongation and leaf area spatial distribution. Direct soil moisture measurements were taken and related to fascicle growth during the third growing season.

5.2.1.1 Elongation of current season's fascicles and its relationship to soil moisture

In September of the third growing season, four trees spanning a range of height sizes in each clone in a weeding treatment for each replication (144 trees) were selected. Ten fascicles in each current season's growing tip (main leader) were marked at the beginning of the growing season just as the needles emerged from the sheath (less than 5 mm long). The fascicle positions were permanently marked with water-based paint. One dot of paint was carefully applied just above the basal sheath of the fascicles. Care was taken to ensure that the paint did not cause needles to stick together and lead to distorted needle growth. This exercise was repeated every 4 weeks from September until April (except mid January) when needle elongation had almost ceased. At each date fascicle length was measured (Figure 5.1).

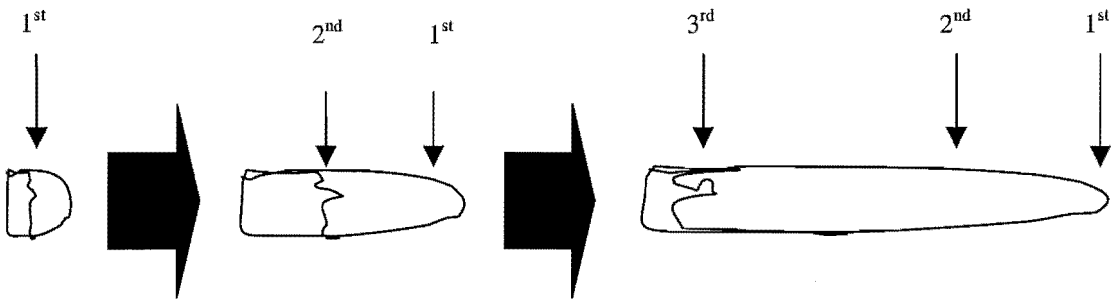

Figure 5.1: Diagrammatic representation of needle elongation, arrows show points where paint was applied on subsequent dates during the growing season. The most recent marking is closest to the basal sheath.

Plots of needle elongation versus time in months were plotted and appropriate functions describing needle growth were fitted (e.g. logarithmic and polynomial functions). Logistic models of the general form,

$$Y = \frac{\alpha}{1 + \beta * \exp(-\gamma * X)} \qquad (5.2)$$ (Hunt 1982);

where,

Y = needle length, X = time in months and α, β and γ are coefficients to be estimated by non-linear least squares in SAS were given first priority as they had been successfully used by other researchers previously (e.g. Kinerson *et al.* 1974, Rook *et al.* 1987, Bandara 1997).

Direct soil moisture measurements were taken in one block at the study site during the summer months (October 1998– March 1999) of the third growing season. Two weeding treatments, completely weed free (Wc9) and the control (Wc0.03) were used. A total of 90 samples (3 cm cores) were randomly taken at depths of 0-10, 10-20 and 20-30 cm (45 in each treatment i.e. 30 in each depth category), (Nugroho 1999). The fresh weights of the samples were determined. The samples were then dried in an oven at 80 °C to constant weight. The gravimetric percentage moisture content on a dry weight basis for each sample was then calculated thus:

$$Percent\ water\ content = \frac{fresh\ weight - oven\ dry\ weight}{oven\ dry\ weight} \times 100 \qquad (5.3)$$

No other data on moisture indicators (e.g. predawn needle water potential, stomatal conductance) was measured in this study. Weather variables e.g. monthly rainfall or temperatures were not also measured. Soil moisture measurements were plotted against needle elongation.

5.2.1.2 Leaf area (LA) and specific leaf area (SLA) spatial distribution

The objectives of this study were to;

1) investigate leaf area and specific leaf area spatial distribution within the crown, and

2) develop regressions for leaf area versus leaf weight (used to estimate total tree leaf area from leaf weight).

In the winters of 1997, 1998 and 1999, fully expanded fascicles were collected from a total of 432 trees. Four trees spanning a range of sizes were chosen from each of clones 1, 2 and 3 in a weeding treatment, giving a total of 144 sample trees in any one winter sampling date. Fully expanded fascicle samples were collected from five crown positions on the trees to investigate leaf area spatial distribution within the crowns (Figure 5.2). The positions were: 1) 2-year-old fascicles on the main leader; 2) 1-year-old fascicles on the main leader; 3) 2-year-old fascicles on first order branches at the bottom of the crown; 4) 1-year-old fascicles on second order branches at the bottom of the crown; and 5) 1-year-old fascicles from branches in the upper part of the crown (above 75% tree height). Sample points were located so as to account for physiological differences due to crown position and needle age effects (Beets and Lane 1987, Grace *et al.* 1987a,b, Dalla-Tea and Jokela 1991).

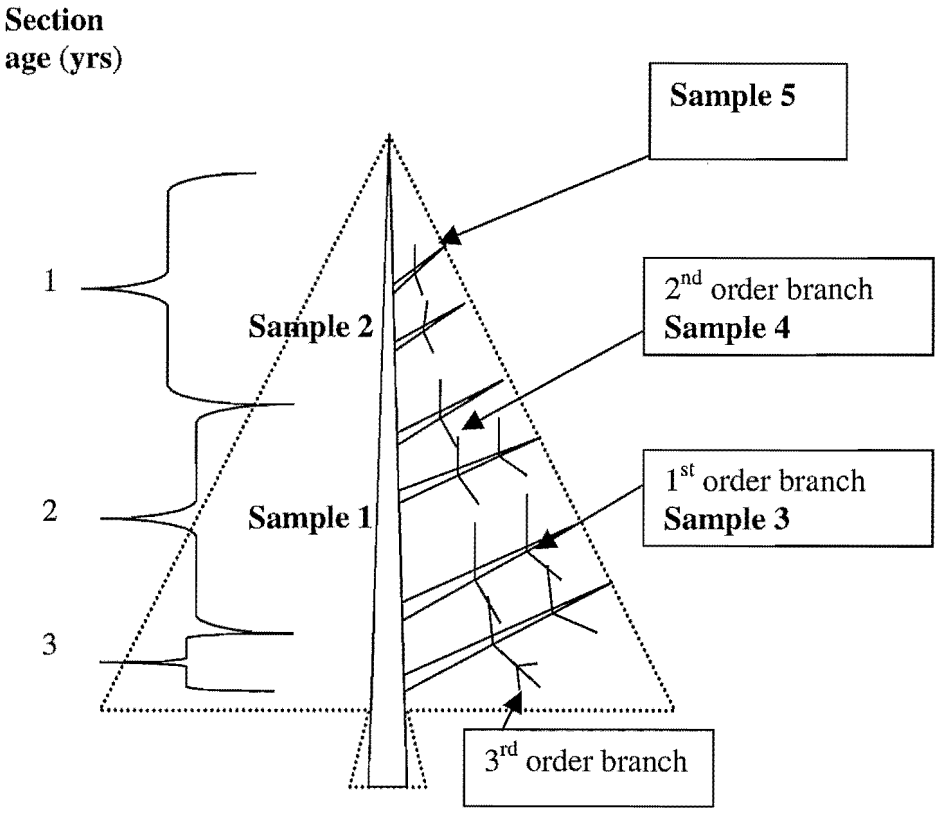

Figure 5.2: Leaf area sample points within the crown.

Four fascicles per tree per crown position were cut off at the base of the basal sheath. The fascicles from the different trees were pooled together if they came from the same treatment and clone and same crown position. The entire fascicles (20 to 30) were wrapped loosely and stored in a chilly bin to avoid desiccation. It was not possible to collect samples in positions 4 and 5 from trees in weedy plots because the needles in these positions were either too small or absent.

In the laboratory the length of each needle was measured while they were still intact in the sheath prior to volume estimation. The individual lengths were summed up to give cumulative length (L). The needle samples were then tied loosely together using a thin 5 amp fuse wire to avoid trapping any air bubbles. The volume of the needle samples was determined to the nearest 0.05 ml by displacement method (Johnson 1984) using a 2.0 ml syringe with 40 graduations. The volume of the wire was later subtracted to remain with needle volume of the sample (V). Total surface area of all sides (LA) was calculated using the equation by Johnson (1984):

$$LA = 2L\left[1+\frac{\pi}{n}\right]\sqrt{\frac{Vn}{\pi L}} \qquad (5.4)$$

where;

LA = total surface area all sides (cm^2),

V = displaced volume of needle sample (cm^3)

n = number of needles per fascicle, and

L = cumulative needle length of needles in the sample (cm).

The samples were oven-dried at 80 ^{o}C to constant weight and their specific leaf area (SLA, cm^2/g) was calculated using the formula;

$$SLA = \frac{Leaf\ area\ (cm^2)}{Leaf\ weight\ (g)} \qquad (5.5)$$

5.2.2 Crown structure and above ground allocation patterns

The objectives of this part of the study were; 1) to quantify clonal responses to variable weed competition gradients in terms of crown structure variables namely, whorl numbers, branch lengths and branch orders and 2) to quantify above ground allocation to stem, branches and foliage.

5.2.2.1 Crown structure

During the winters of years 1 and 2, four trees spanning a range of height sizes were chosen from clones 1, 2 and 3 in all the weeding treatments and by replications (a total of 144 trees). The following crown structure variables were assessed;

1) total number of whorls and their heights above the ground,
2) number and length of all branches which were at least 3 cm long (in the control treatment most current season branches were about 3 cm long) were assessed, and
3) branch order of production, and diameter at the point of inception.

Whorl height above ground was measured to the base of the whorl and to the nearest cm. Branch length was measured to the nearest cm on the upper part of the branch. Branch age, whorl cycle and order of production were determined in similar fashion to Rook *et al.* (1987), (Figure 5.3).

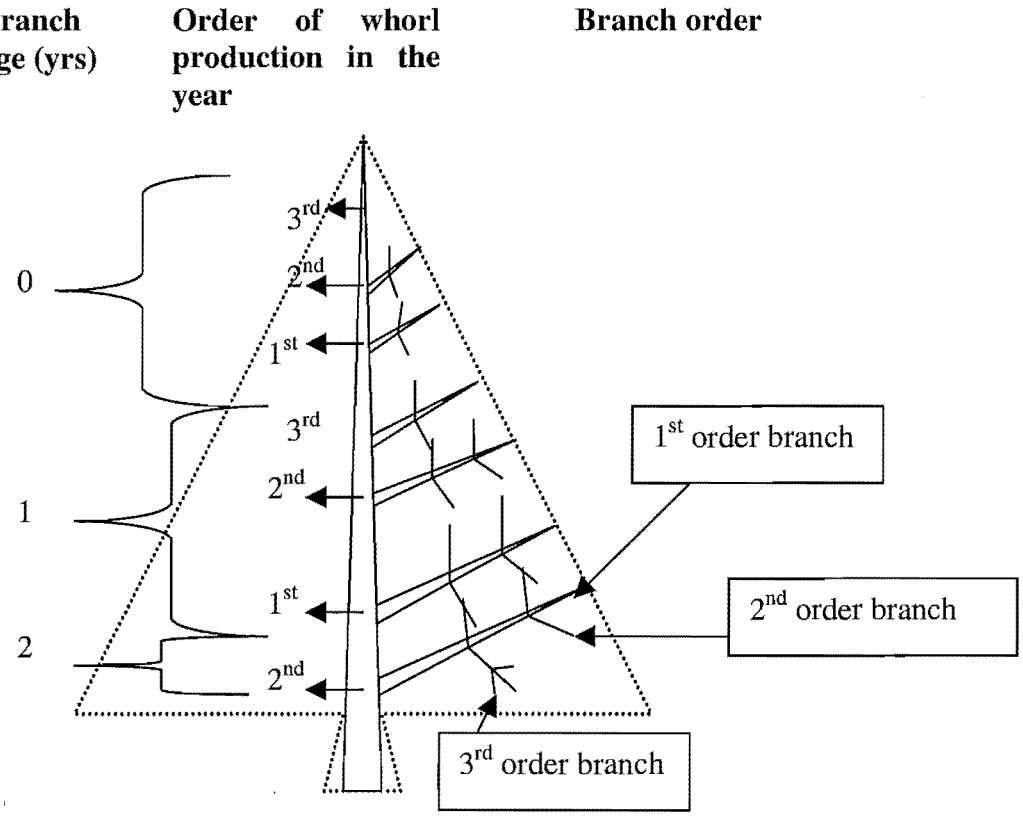

Figure 5.3: Diagrammatic representation of the classification of branches by age, whorl cycle and branch order (adapted from Rook *et al.* 1987).

5.2.2.2 Using limited destructive sampling procedures to estimate tree biomass

Above ground tree biomass was measured for a total of 60 trees set aside for the purpose. Fifteen trees were harvested at the end of the first year, another 15 in the second year and 30 at the end of the third year of growth. All trees for destructive sampling grew under 1 m diameter spots in years 1 and 2 of the study. During year 3 some trees had increased weed free area to 2 m spots. Therefore, of the 30 trees sampled in year 3, 15 trees had 1 m spots treatment since planting, while the remaining 15 had 1 m spots in years 1 and 2, and 2 m spots in year 3 (1998/1999 growing season).

In the field, trees were cut at ground level (0-2 cm above the soil) and separated into stem and branches. The stem and branch sections were then chopped into manageable sizes and bagged carefully into large clearly labeled paper bags. The samples were taken to the laboratory. Labels showed the weeding treatment, clone,

tree number and tree section (i.e. branch or stem). Before the trees were harvested their crown images were taken using a digital camera. The height (H) and ground line diameter (GLD) of each tree was also measured. Fascicle samples for estimation of leaf area and specific leaf area were also collected from similar positions as described earlier (see section 5.2.1.2).

In the laboratory the stem and branch portions were separated into foliage and woody components. All components were clearly labeled and oven dried at 80 ^{o}C to constant weight. The dry weights of all the foliage, stem wood (excluding foliage) and branch wood (excluding foliage) were determined for each harvested tree. Dry weight was measured to the nearest 0.01 g. All stem and branch biomass measurements were inclusive of tree bark.

Regression equations (SAS/STATS 1996) were developed for foliage dry weight versus crown photo area and total tree biomass versus crown photo area. Regressions of stem wood versus GLD^2*H and branch wood versus GLD^2*H were developed for trees in the 1 m diameter spot weeding treatment as this was the only treatment fully represented in the biomass data. The developed regressions were used to estimate total tree foliage weight and total tree biomass of standing trees in the experiment. There were concerns about relying on relationships derived from trees grown in 1 m diameter spots and then extrapolating this to other plot sizes. This could be risky given the large differences in tree size brought about by the weed control treatments. However, this was the only data available from this study.

5.2.3 Image Analysis: A non-destructive technique for estimating above ground tree biomass

Crown photographs of all trees were taken using a digital camera (Olympus CAMEDIN C-840L) at ages 1, 2 and 3. Crown photo areas were calculated using Metamorph image analysis software (Universal Imaging Corporation 1995). Three crown photo area readings were taken from each image and the average of the three

was used for the tree. The images were prepared for analysis by calibrating, processing and thresholding as described in the following sections.

5.2.3.1 Image processing

Before images could be measured, they were converted into a format which could be displayed and analysed in Metamorph, an image analysis package. This involved adjusting the digital contrast, colour encoding and thresholding. Colour encoding enabled conversion of the 24-bit colour images into 8-bit 3-plane images (Universal Imaging Corporation 1995).

5.2.3.2 Calibrating images

Calibrating image distances was achieved by using a specified distance in the image window (graduated height pole) and setting this to some specified units per pixel. Four sections of the pole (20 cm) were set equal to a number of pixels in the image. The distances were therefore converted from pixels to centimeters.

5.2.3.3 Sharpening

This command was useful to accentuate the edges of the images so that finer details were enhanced without change to the gray scale value. A low filter was used to sharpen the images.

5.2.3.4 Marking an active region

Sometimes parts of an image could not be accurately separated from the background during thresholding. In such cases, better separation was achieved by first tracing out the crown profile with a line (using the line draw tool).

5.2.3.5 Thresholding

Images were thresholded to separate objects to be measured from the general background. This was done in Metamorph by putting a red overlay on the objects while the background areas remained gray. The images were then ready for area calculations.

5.2.3.6 Crown photo area measurements

Once the images had been satisfactorily processed, area measurements were made. Active regions were marked and highlighted on the thresholded images by tracing out the tree crown form. The area of the active region was measured by choosing "Measure single object" from the "Measure" menu drop-down list in Metamorph. To get true object area, hole areas (areas within the active region which were not thresholded) were subtracted from the total object area. Distances were calibrated to centimetres, so areas were in square centimetres.

5.2.3.7 Factors affecting accuracy and precision of estimates

There were two main factors determining the accuracy and precision of area estimates.

1) Thresholding – had the most significant influence on accuracy and precision. How well an image was thresholded depended on familiarity with Metamorph and experience. These two factors improved consistency and thereby increased precision and accuracy. Inexperience led to judgement errors especially regarding image outlines and/or thresholding levels.

2) Processing – adequate processing made it easier for image borders and outlines to be identified easily. Sufficiently processed images showed sharp features when thresholded. Poorly processed images tended to have blotched edges. This led to bias in area estimates with higher readings often being common.

Necessary steps were taken to avoid bias as outlined below (section 5.2.3.8).

5.2.3.8 Remedy: minimizing measurement errors

In this study well-laid-down procedures were adhered to in order to reduce errors and improve precision and accuracy of area measurements.To minimise errors:

1) the same person did all the area measurements all the time;
2) training runs with metamorph were conducted to acquaint the person doing the measurements with the system prior to any analyses; and

3) three area readings were taken, at different times, for each image and the mean value used. Area values that differed by more than 1 % within a set were repeated.

There were concerns that as trees got bigger mutual shading between trees could result in errors in area estimates (Richardson pers. comm.). However, the trees in this study were yet to close canopy and therefore no such errors were incurred.

5.2.4 Data analysis procedures

Analysis of variance (ANOVA) was carried out on all the assessed variables using the General Linear Models (GLM) procedure in SAS (SAS/STATS Inc. 1996). Significant variables and their interactions were subjected to hypothesis testing using the appropriate plot and subplot error terms. Variables that were not significant at the 0.05 probability level were excluded from further analyses.

Hypotheses tested included:

H_{01}: there were no significant differences in leaf area spatial distribution within crowns;

H_{02}: there were no significant differences in specific leaf area in different crown regions;

H_{03}: there were no significant differences between clones and weeding treatments for total tree leaf weight (estimated using crown photo areas), above ground allocation, needle elongation.

The alternative hypotheses were that significant differences were present in the measured variables. All tests were carried out at the 0.05 probability level.

Regressions of tree leaf weight versus leaf area, needle elongation versus time, foliage weight versus crown photo areas, stem wood versus GLD^2*H and branch wood versus crown photo areas and/or GLD^2*H were fitted to data. Before any models were fitted to data scatter diagrams from the Gplot procedure in SAS (SAS/STATS Inc. 1996) were plotted to observe the kind of relationships that existed

between the dependent and independent variables of interest. The plots were also important in identifying any special cases or "outliers". Appropriate model formulations (linear and non-linear) were then made. Models tried included the following;

1) $Stem\ weight = \alpha + \beta * (D^2 * H)$ (5.6),
2) $Stem\ weight = \alpha * (D^2 * H)^{\beta}$ (5.7),
3) $Branch\ \ weight = \alpha + \beta * (D^2 * H)$ (5.8),
4) $Foliage\ \ dry\ \ weight = \alpha * (Crown\ \ \ photo\ \ \ area)^{\beta}$ (5.9),
5) $Total\ tree\ \ dry\ \ weight = \alpha * (Crown\ \ \ photo\ \ \ area)^{\beta}$ (5.10).

In all cases α and β were coefficients estimated from least squares procedures in SAS. Non-linear models were fitted using the non-linear procedure (Proc NLIN) in SAS, while GLM (SAS) was used for linear models. Models were fitted to all the data with weeding treatments, genotype and their interactions as dummy variables.

5.3 RESULTS

5.3.1 Foliage growth dynamics and leaf area spatial distribution

5.3.1.1 Needle elongation and its relationship to soil moisture content during the 3rd growing season

Competition from weeds reduced needle growth significantly ($P < 0.0001$) during the growing season (Figure 5.4). Trees growing in weedy plots had delayed needle emergence. Meanwhile needle emergence times for trees in all the other treatments were similar. Growth was faster early in the season (October to November). However, in mid-summer (December and February) the growth rate slowed down considerably as shown by the slump in the lines (i.e. a lower gradient[1]) (Figure 5.4).

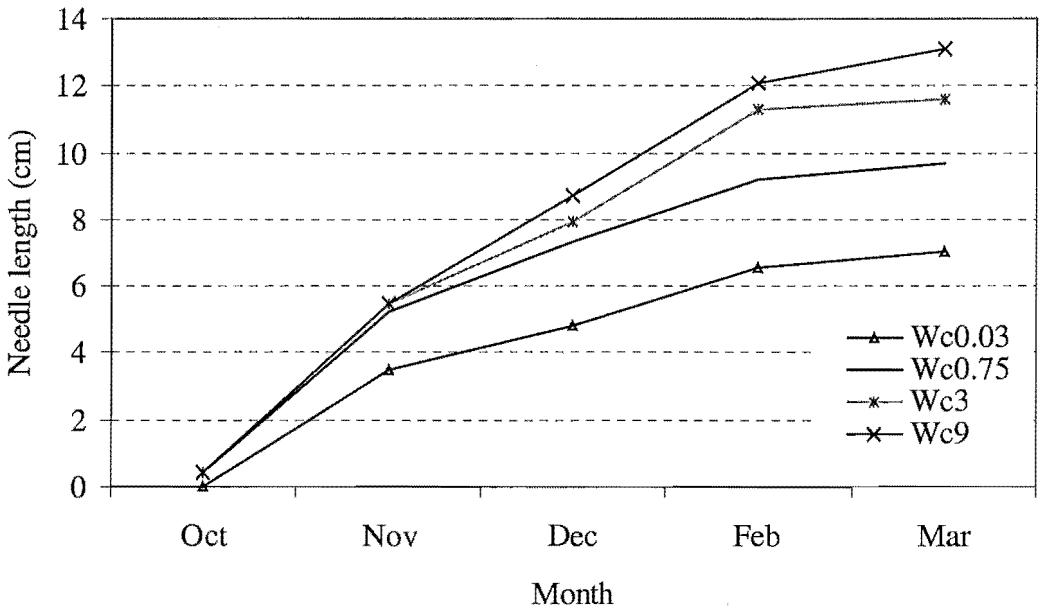

Figure 5.4: Average fascicle length by time (month) since emergence for weeding treatments (note delayed emergence of fascicles in the control treatment, Wc0.03).

[1] Note: Due to lack of measurements in mid-January, the slope between December and February is actually much lower than it appears in the figures.

All 3 clones had similar times of needle emergence (Figure 5.5). However, differences in the rates of needle growth were evident within the first month of measurement (November). These differences were maintained throughout the growing season. Thus clone 3 had longer fully expanded fascicles at the end of the growing season than the other 2 clones investigated (Figure 5.6).

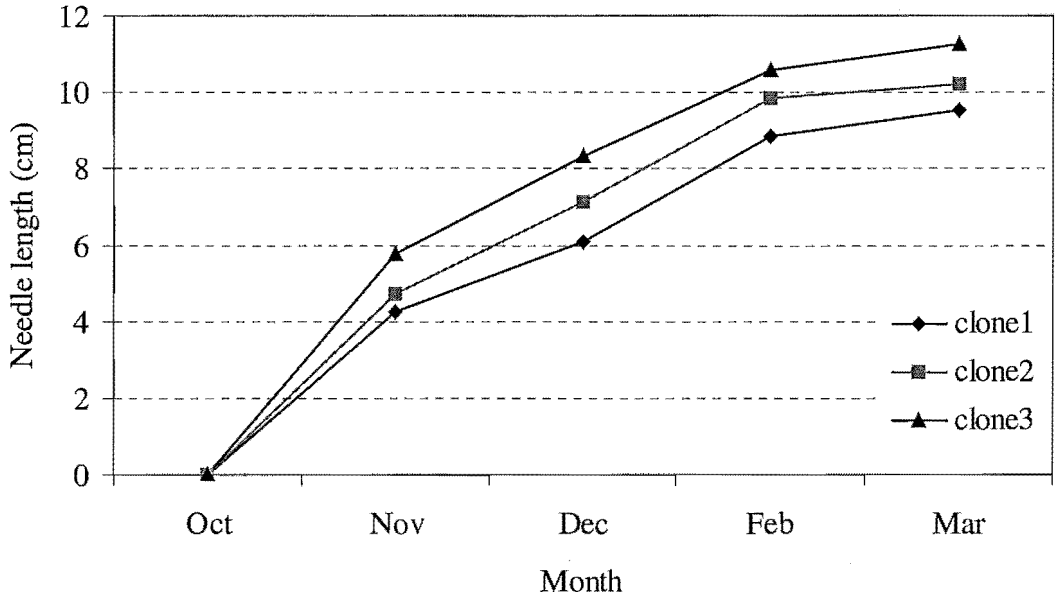

Figure 5.5: Average fascicle length by time since emergence for clones.

Final needle lengths for weeding treatments and clones are shown in figure 5.6.

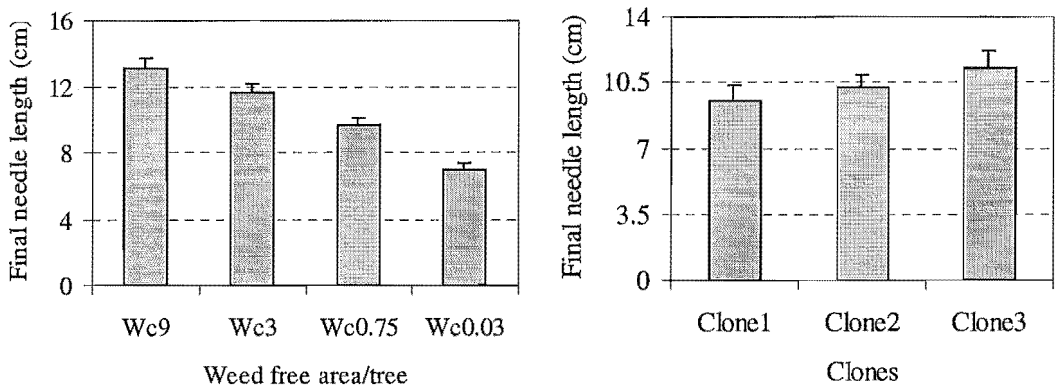

Figure 5.6: Final needle length for weeding treatments and clones.

Needle elongation during the season was best described by a logarithmic function;

$$Length = \alpha + \beta * \log(Time) \quad (5.11)$$

where;

$\alpha = 6.3721+(-2.1248)*V_1+(-1.1444)*V_2+(-1.8524)*M_1$ and

$\beta = 4.1865+(-1.9847)*M_1+(-1.1730)*M_2+1.1824*M_3$.

α and β were regression coefficients and V_1 and V_2 were dummy variables for clones 1 and 2. M_1, M_2 and M_3 were dummy variables for weeding treatments Wc0.03, Wc0.75 and Wc9 respectively. Residual plots showed little bias with all residuals lying between ±1.28 cm (Figure 5.7 to 5.10).

Table 5.1: Final selected model outputs for needle elongation model.

Needle elongation	Residual MSE	Mean	Skewness	Kurtosis	Range of residuals
(3rd growing season)	0.3503	0	0.27026	-0.92216	-1.07 to +1.28 cm

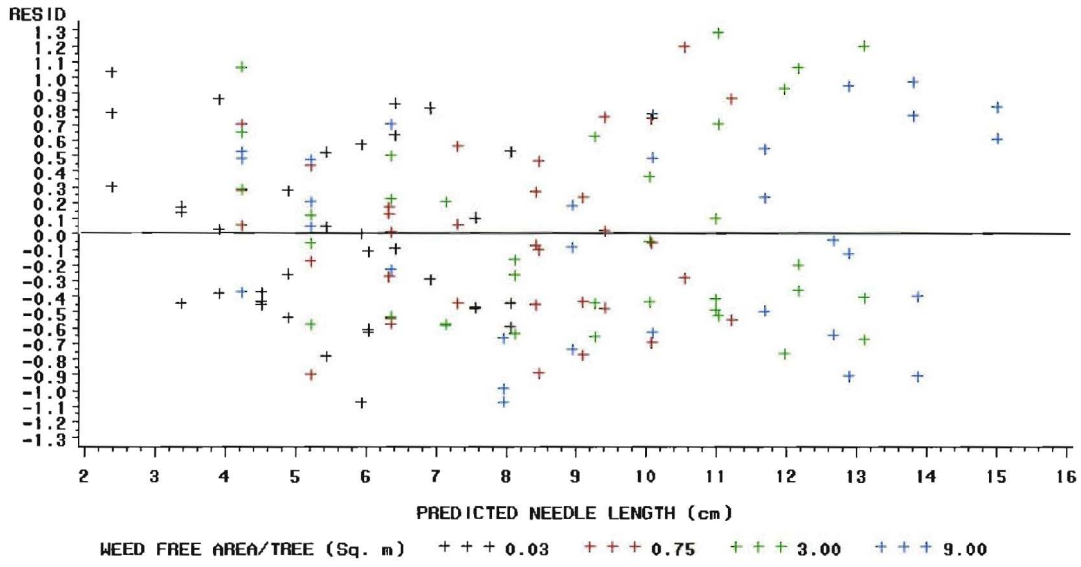

Figure 5.7: Plot of residuals versus predicted for needle elongation (cm) during the 3rd growing season.

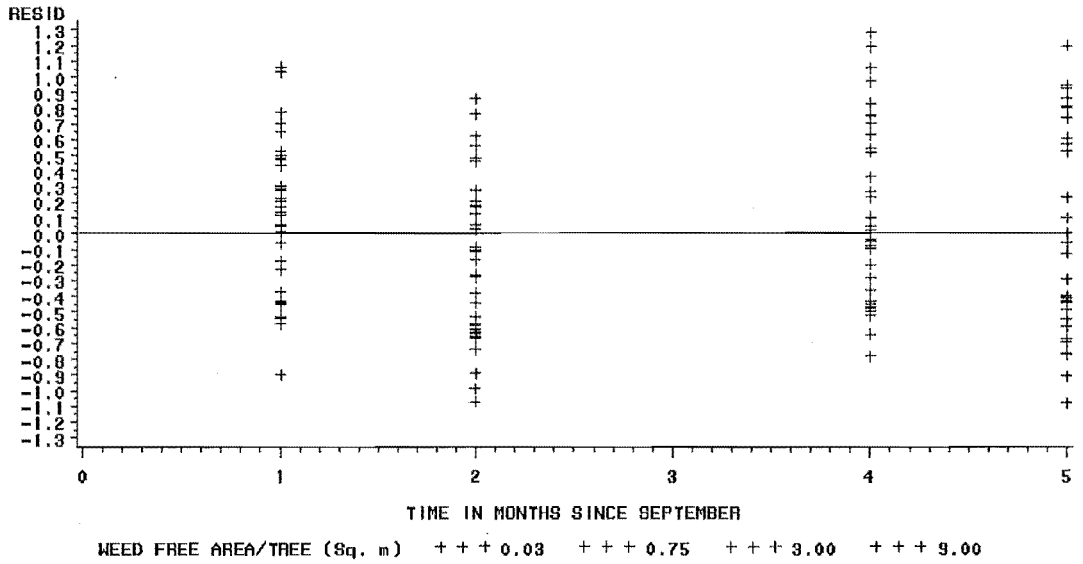

Figure 5.8: Plot of residuals versus time in months for needle elongation during the 3rd growing season (from September).

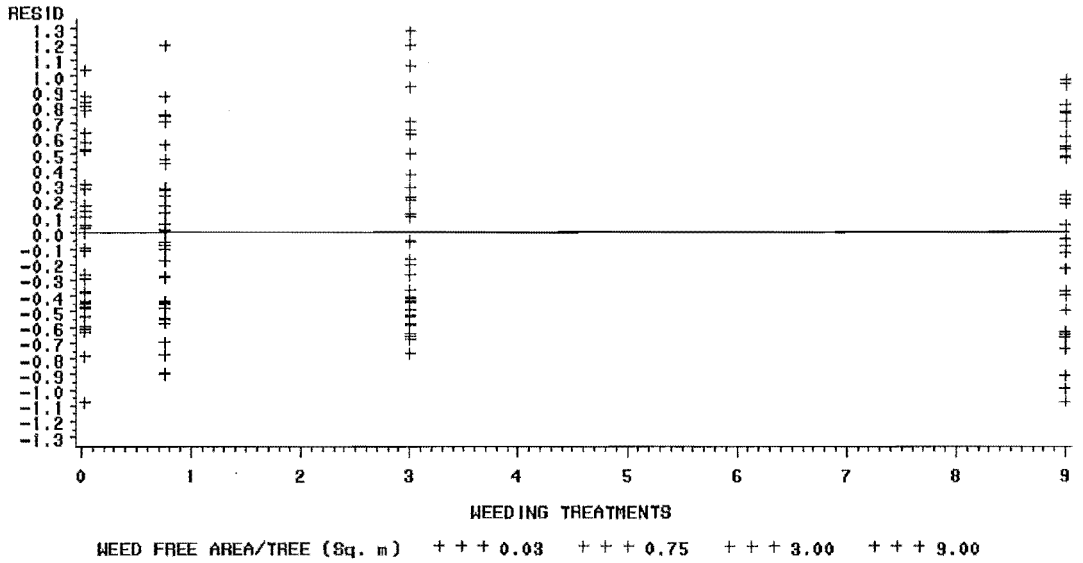

Figure 5.9: Plot of residuals versus weeding treatments for needle elongation during the 3rd growing season.

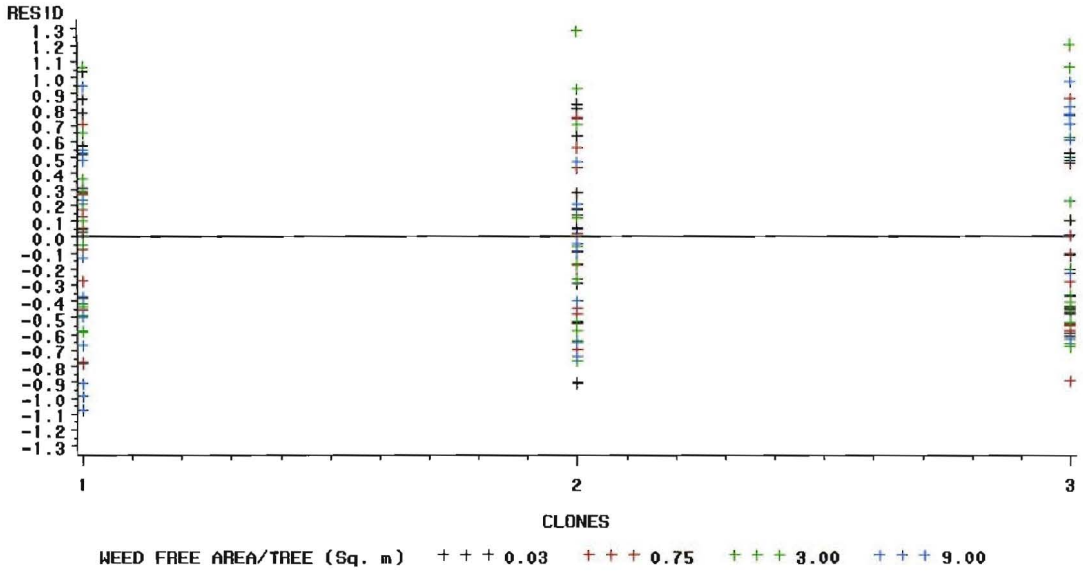

Figure 5.10: Plot of residuals versus clones for needle elongation model during the 3rd growing season.

Logistic models (e.g. Kinerson *et al.* 1974, Hunt 1982, Rook *et al.* 1987, Bandara 1997) did not fit well to the data.

The deceleration in growth coincided with periods of acute soil moisture levels recorded at the site during mid-summer (Figure 5.12) and this may have contributed to reduced needle development late in the season. Older needles in Wc0.03 were also chlorotic. Direct soil water measurements during the main growing season showed that more moisture was available in deeper soil horizons (>10 cm depth) in Wc9 than in Wc0.03 (Figure 5.11). Complete weeding resulted in significantly more moisture being available in the soil ($P<0.0042$) for all measurement times (Figure 5.12). There was a significant ($\alpha = 0.1$) weeding-by-depth interaction ($P<0.0539$).

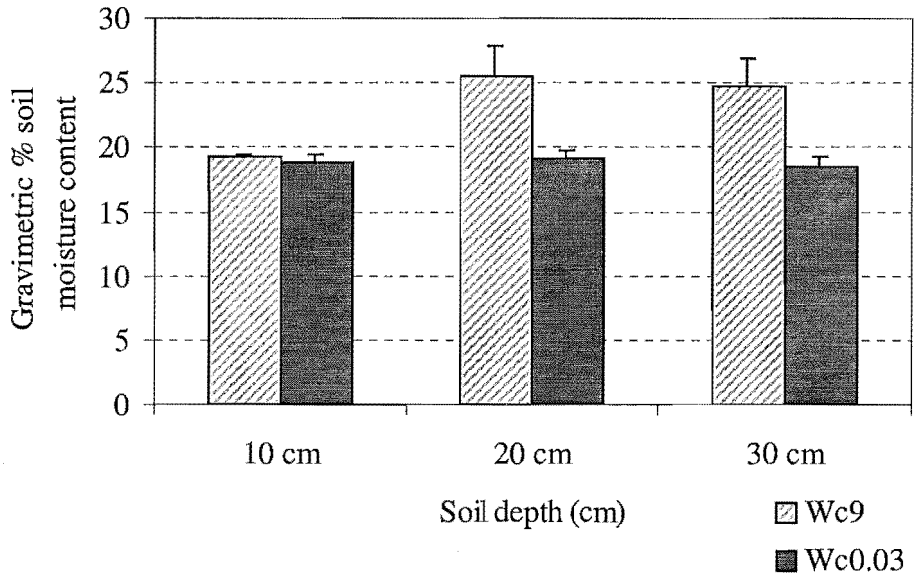

Figure 5.11: Soil moisture content of the control and complete weeding treatments at the three depths during the third growing season.

The lowest moisture readings were recorded in mid-summer (February) for all depths (Figure 5.12). Needles in treatment Wc9 continued to grow at higher rates than those in Wc0.03 even during the period when soil moisture was at its lowest levels (Figure 5.12).

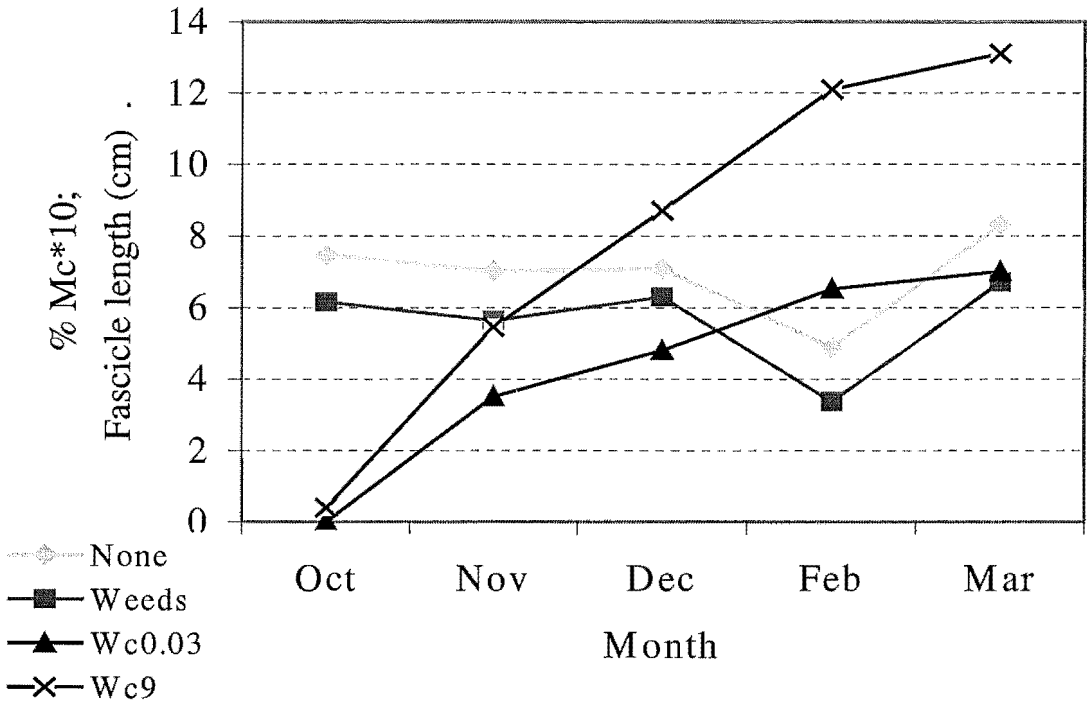

Figure 5.12: Percent gravimetric soil moisture (%Mc*10) variation and needle elongation for the period October to March (Wc0.03 = needle growth in the control, Wc9 = needle growth in complete weeding). "None" and "weeds" represent complete weeding and the unweeded control treatments respectively. No measurements were taken in January.

5.3.1.2 Leaf area versus leaf weight relationships

A strong linear relationship existed between leaf area and leaf weight (Figure 5.13). A linear equation allowing for differences in slopes (β) and intercepts (α) for weeding and clones was fitted to the pooled data (R^2 = 0.9457, 386 observations);

$$Foliage\ Area = \alpha + \beta * Leaf\ dry\ weight \qquad (5.12)$$

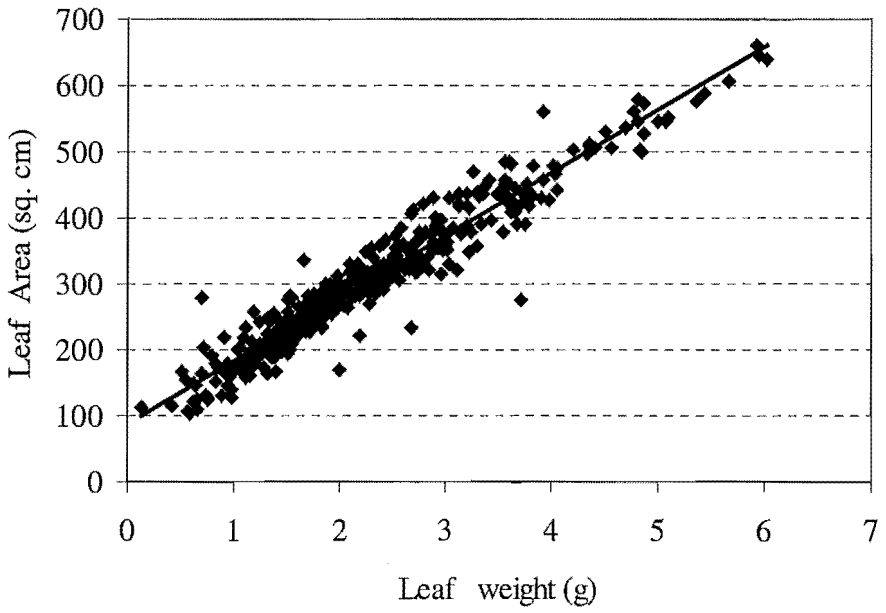

Figure 5.13: Relationship between leaf area (cm^2) versus leaf weight (g).

The intercepts of Wc9 ($P < 0.0137$) and Wc3 ($P < 0.0001$) were significantly higher than those of Wc0.75 and Wc0.03, while Wc0.03 had a significantly lower slope ($P < 0.0419$). Clone 3 had a significantly ($P < 0.0001$) higher intercept than the other two clones (Table 5.2), while clone 1 had significantly the lowest slope ($P < 0.0026$). Tree age and crown position had statistically significant ($\alpha = 0.05$) effects on the relationship.

Table 5.2: Final selected model outputs for leaf area versus leaf weight.

Variable name	Intercept estimate (α)	Slope estimate (β)
Clone1	87.922	88.562
Clone2	105.216	85.993
Clone3	112.305	87.520
Wc9	139.773	86.106
Wc3	124.710	85.765
Wc0.75	112.305	87.520
Wc0.03	113.353	72.391

5.3.1.3 Leaf area and specific leaf area spatial distribution

Total fascicle leaf areas varied significantly with crown position ($P<0.0001$, crown positions were shown in Figure 5.2, section 5.2.1.2), weeding treatments ($P<0.0001$) (Figure 5.14) and genotype ($P<0.0002$) (Figure 5.15). Specific leaf area for the individual leaf - age categories differed significantly between weeding treatments ($P<0.0006$), as well as between crown positions ($P<0.0001$). The clone by position interaction was significant ($P<0.0182$).

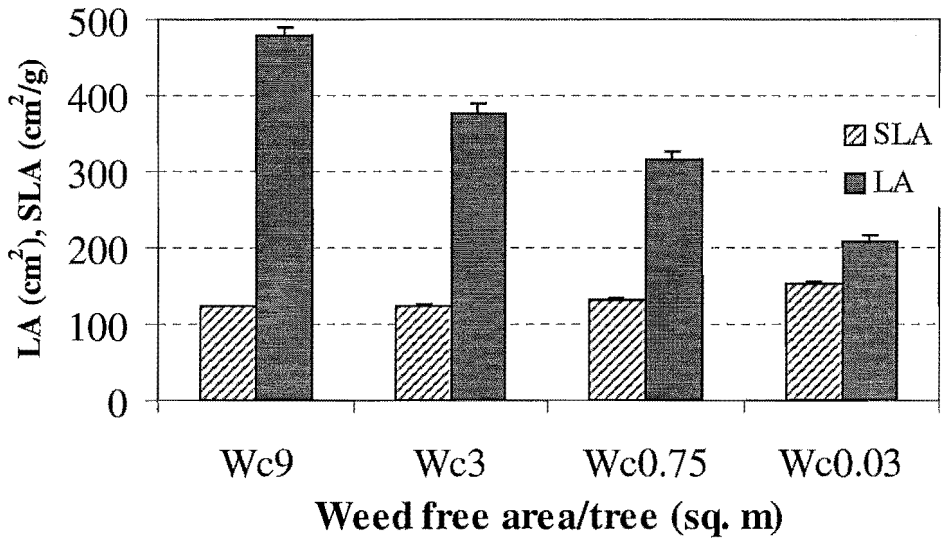

Figure 5.14: Sample leaf area and specific leaf area by weed free area/tree.

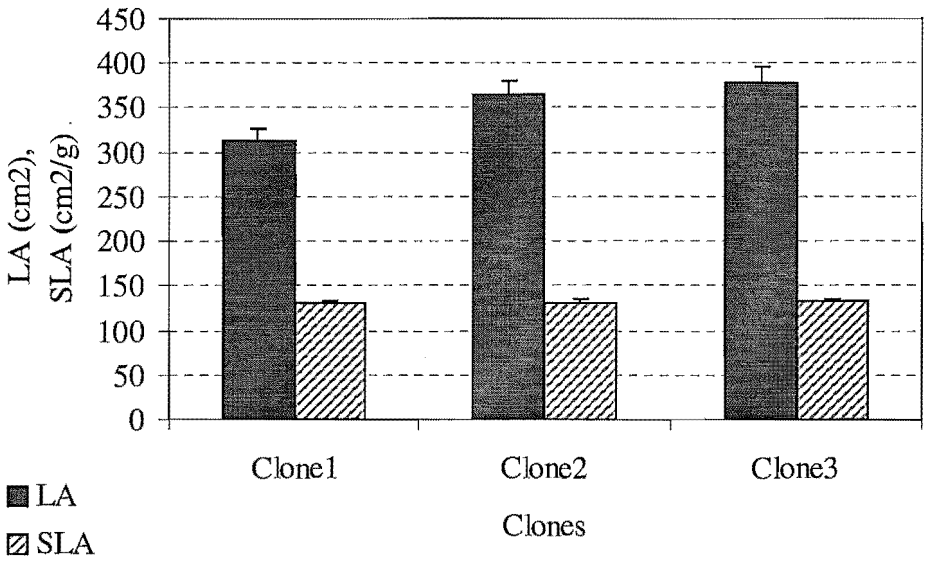

Figure 5.15: Sample leaf area and specific leaf area for clones.

All clones differed significantly (P = 0.05) in their leaf areas but not specific leaf areas. One-year old fully expanded needles on the upper stem (positions 2 and 5, see Figure 5.2) had higher leaf areas than other positions. Needles on the lower crown (positions 3 and 4, see Figure 5.2) had the lowest leaf areas irrespective of age. Fully expanded current season fascicles in the control plots had only 43%, 55% and 65% the leaf areas of their counterparts in Wc9, Wc3 and Wc0.75 respectively.

5.3.2 Crown structure

Significant differences in mean whorl numbers (P<0.0012), first order branch numbers (P<0.0007) and branch lengths (P<0.0002) were observed between weeding treatments. Weeding also influenced the elongation of second order branches (P<0.0064). Clonal differences were present for whorl numbers (P<0.0002), first order branch numbers (P<0.0001) and branch lengths (P<0.0021). Second order branch lengths did not differ significantly between clones. There was no evidence of a weeding by clone interaction for these variables (Kirongo and Mason 1999).

Of the three clones studied, clone 1 had the lowest number of both first and second order branches. Clone 3 had the longest branch network. Meanwhile, trees in the control had the shortest branch length network and a very small number of 2nd order branches (Figure 5.16).

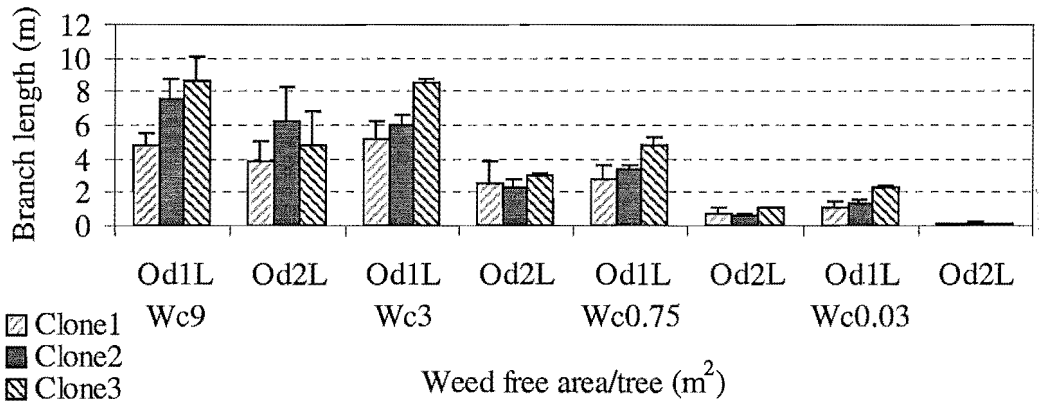

Figure 5.16: Branch length (m) of 1st order (Od1L) and 2nd order (Od2L) branches in clone 1, 2 and 3 by weeding treatment.

Trees growing in weedy plots had an average 2.96 branch whorls compared to 4.88 for Wc0.75, 5.64 for Wc9 and 6.21 for Wc3. Trees in clone 1 and clone 3 growing under 3 m^2 spots had higher mean number of whorls than their counterparts in Wc9 (Figure 5.17).

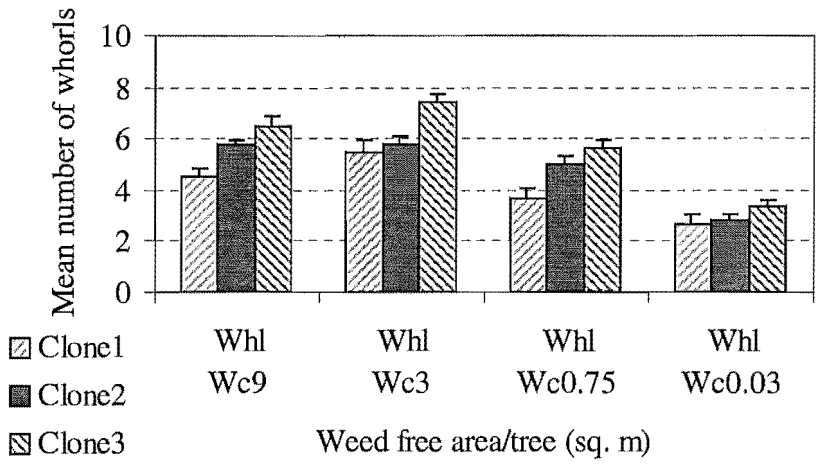

Figure 5.17: Mean number of branch whorls (whl) in clones 1, 2 and 3 vs weeding treatments.

Whorls in the lower third (33 %, Figure 5.18) of the crown had the longest first order branches in the tree. Most second order branches were in the same zone as well.

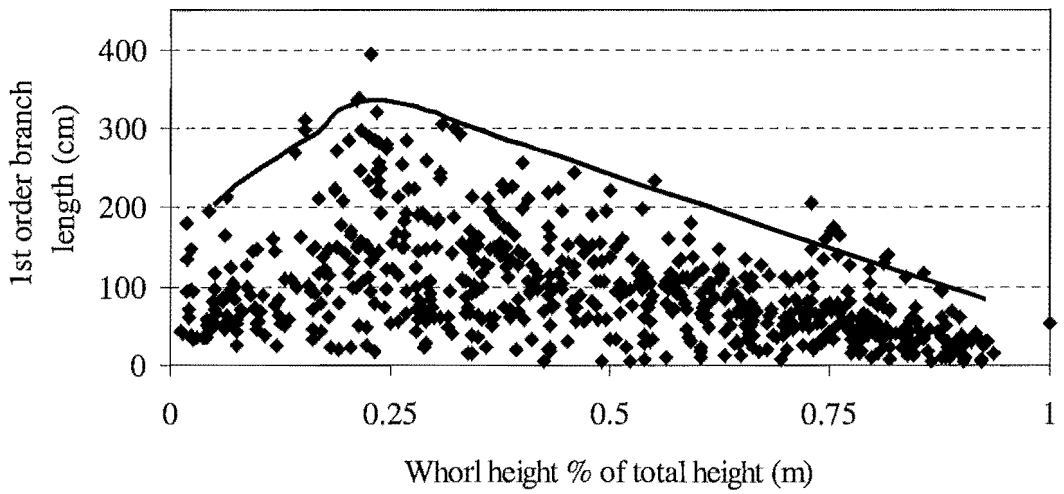

Figure 5.18: First order branch length versus whorl height above ground. (The free hand line is meant to emphasise the shape of the graph).

5.3.3 Above ground allocation patterns

5.3.3.1 Allocation to wood and foliage

In year 1 allocation to foliage was 23 percent in clones 1 and 2 and 36 percent in clone 3, but this increased rapidly to 46-52 percent by year 3 (Table 5.3 and Figure 5.19). Allocation to stem wood and branch wood varied with clone and tree age.

Table 5.3: Mean tree allocation values for clones 1, 2 and 3 during the 3-year study period (Wc3* see foot note).

Component % dry weight by clone (C1-3)	YEAR 1			YEAR 2			YEAR 3 (Wc0.75)			YEAR3 (Wc3)*		
	C1	C2	C3	C1	C2	C3	C1	C2	C3	C1	C2	C3
Foliage	23.2	23.3	35.9	38.2	46.2	47.3	46.4	50.7	52	44.6	47.2	49
Stem wood	-	-	-	34.5	27.4	28.2	30.2	29.2	28.8	31.8	26.7	29.4
Branch wood	-	-	-	27.4	26.3	24.5	23.4	20.1	19.2	23.5	26.1	21.7
Total tree	100	100	100	100	100	100	100	100	100	100	100	100
Mean tree biomass (kg)	.049	.042	.145	.460	.337	.701	1.81	1.43	2.00	2.01	2.03	3.01

* These trees had 1 m spot diameters in years 1 and 2, which was increased to 2 m spot diameters in year 3 only)

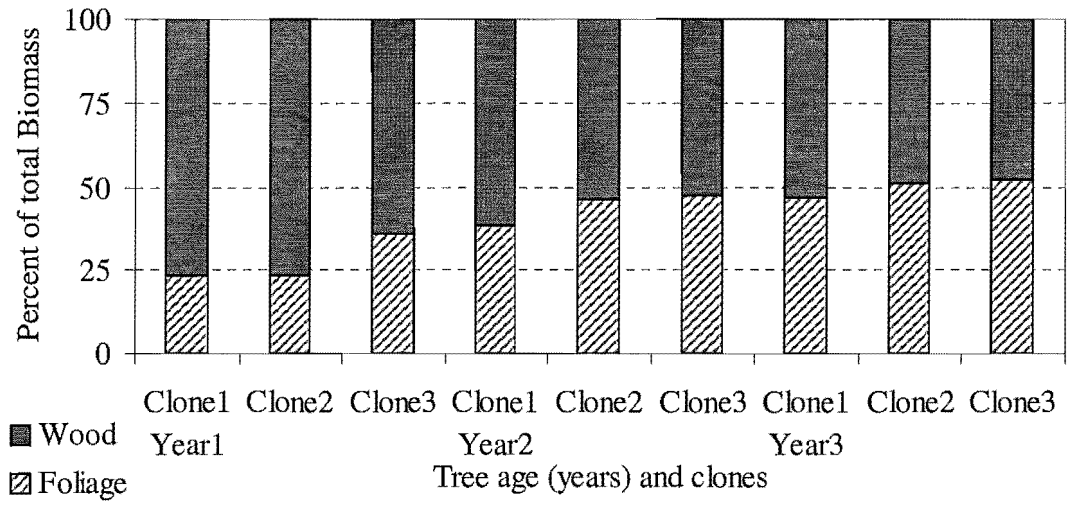

Figure 5.19: Proportional above ground allocation to foliage and woody material during years 1, 2 and 3 (Figure excludes data in Wc3*).

All the three clones allocated more to woody material than to foliage in both years 1 and 2. Clone 3 had higher allocations to both wood and foliage in all the 3 years. By year 3, Clone 3 had shown a different allocation strategy; allocating more to foliage than to wood. Clone 1 was still allocating significantly less to foliage compared to wood, however (Figure 5.20). Increasing spot sizes from 1 m to 2 m diameter at the end of year two was beneficial to clones 2 and 3 but not clone 1. Figure 5.20 makes it clear that clone 3 made the best use of the increased spot sizes during year 3.

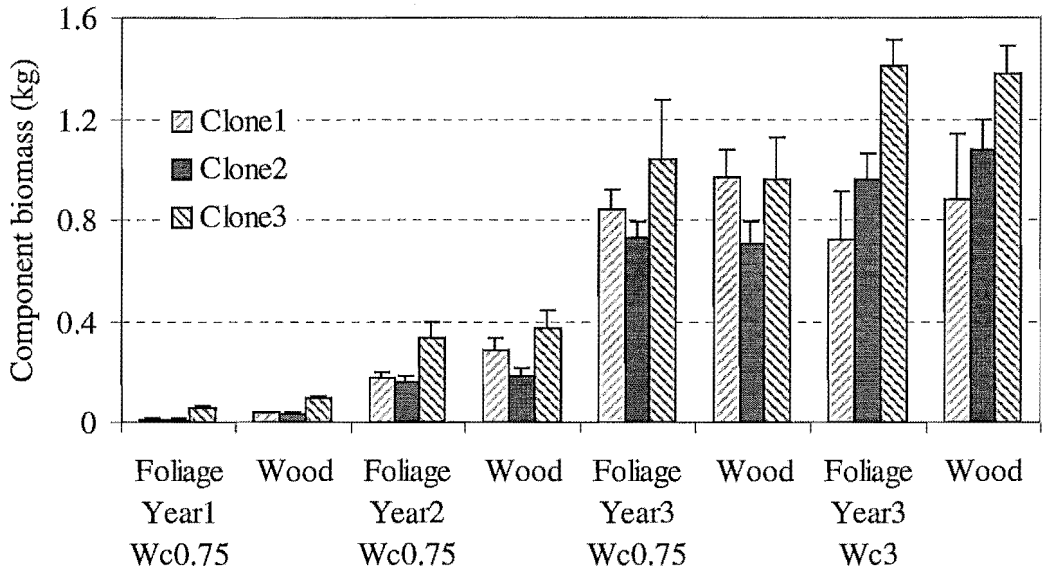

Figure 5.20: Clonal comparisons of allocation patterns to wood and foliage in years 1, 2 and 3.

5.3.3.2 Allocation to stem and branches (inclusive of foliage)

In year 1, 70 percent of the biomass in clones 1 and 2 (55 % in clone 3) was in the stem. However, there was a sharp drop in all clones to only about 35 percent by year 3. Meanwhile, allocation to branches rose accordingly (Figure 5.21).

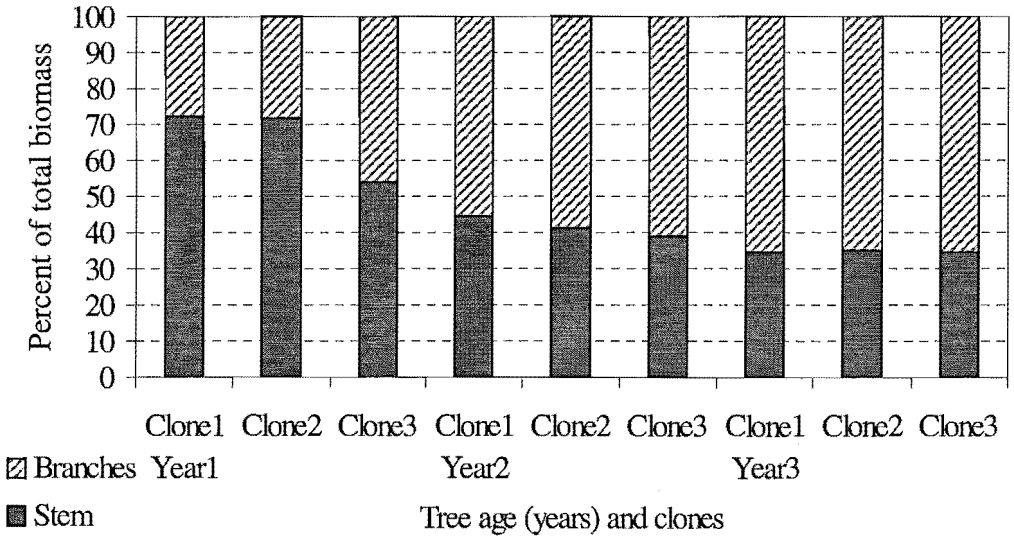

Figure 5.21: Allocation to branches and stems in years 1, 2 and 3 (inclusive of foliage).

5.3.3.3 Proportion of foliage on stem and branches

In year 2 an average 35 % of the total foliage was held in the stems. This figure reduced to 15 % in year 3, while the proportion held by the branches rose accordingly to 85 % (Figure 5.22).

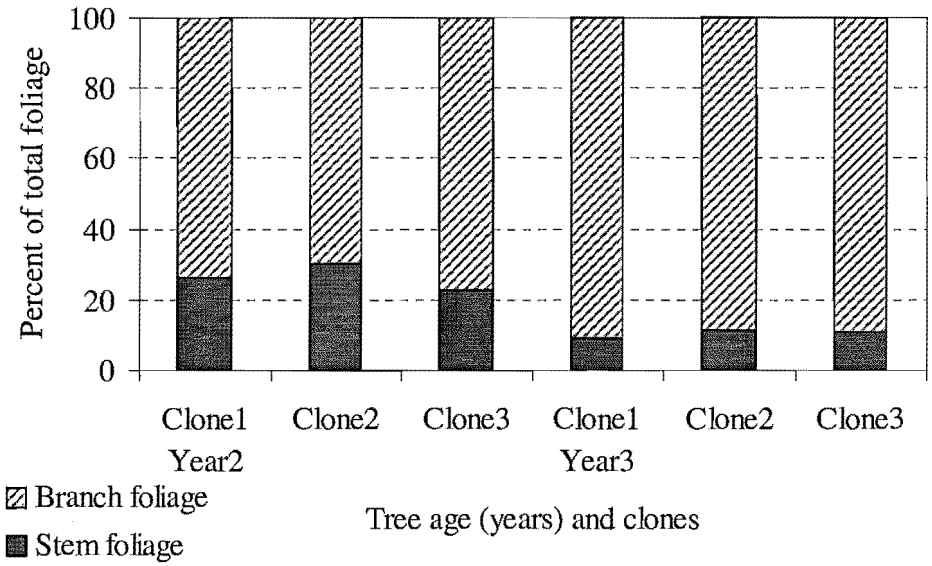

Figure 5.22: Percent proportion of foliage held by branches and stems in years 2 & 3.

5.3.4 Image Analysis

A strong relationship was found to exist between crown image area and total tree foliage weight (Figure 5.23) as well as total tree biomass (Figure 5.26). Both total tree biomass and leaf weight were modelled using exponential equations; 5.13 and 5.14.

$$Leaf\ drywt = \alpha * (Crown\ \mathrm{Im}age\ area)^{\beta} \qquad (5.13)$$

The estimated coefficient values for leaf biomass were,

$\alpha = 1.3193 + 0.4479*V_3$ and $\beta = 1.1864 + 0.2435*V_3$.

V_3 was a dummy variable for clone 3.

For total tree biomass by crown photo area, the function and estimated coefficient values were;

$$Total\ tree\ drywt = \alpha * (Crown\ \mathrm{Im}age\ area)^{\beta} \qquad (5.14)$$

where;

$\alpha = 2.909 + 0.4256*V_3$ and $\beta = 1.276$.

(coefficients and dummy variables are as described earlier).

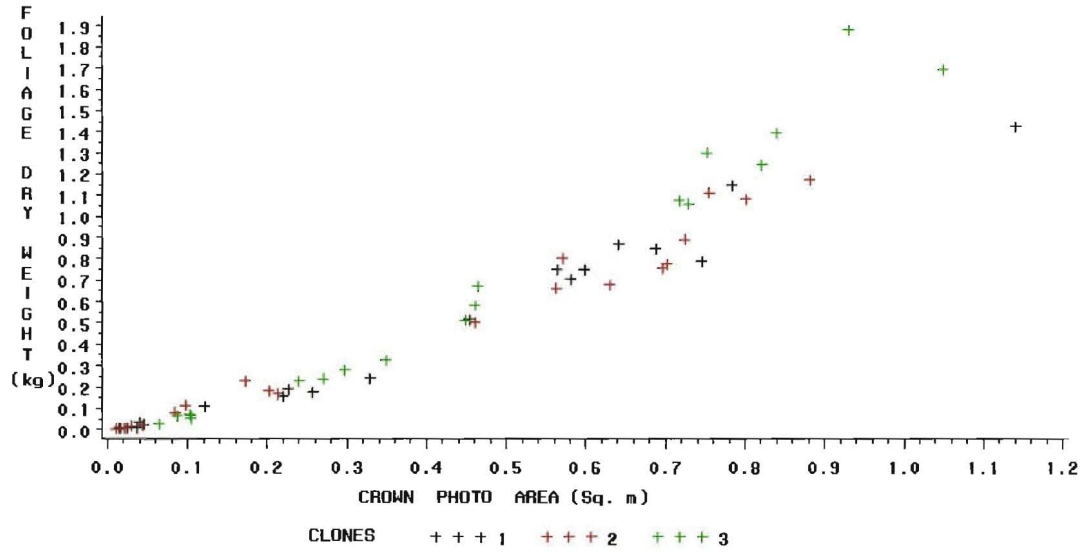

Figure 5.23: The relationship between crown photo areas (m^2) and tree foliage dry weight (kg) (individual tree raw data of destructively sampled trees).

Plots of residuals by predicted values and all independent variables for the foliage dry weight model showed little bias (Figures 5.24 and 5.25). Similar trends showing little bias were observed for the total tree biomass model (Figures 5.27 and 5.28).

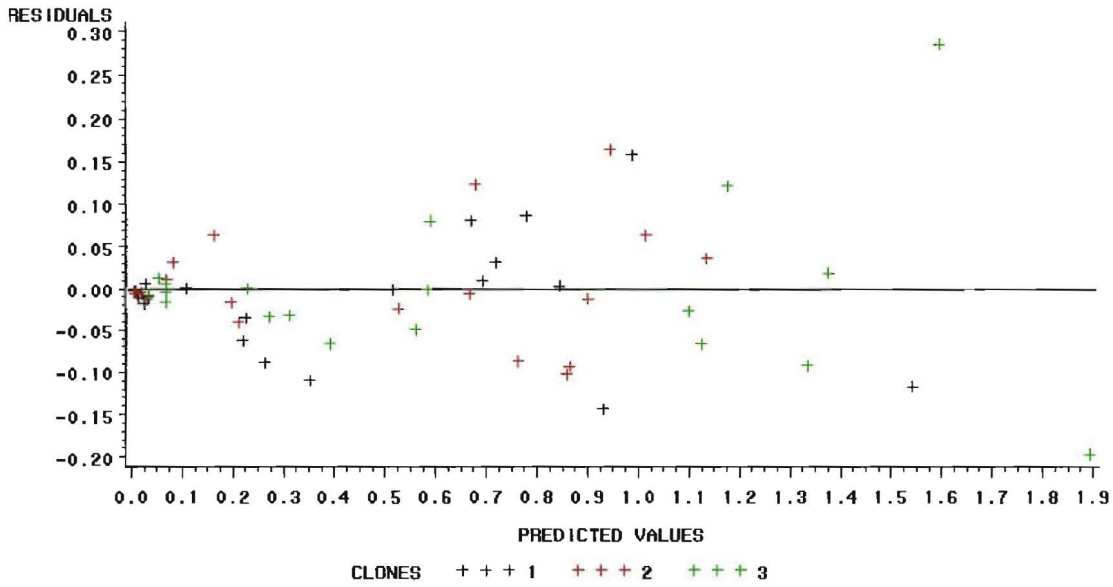

Figure 5.24: Plot of residuals by predicted values for foliage dry weight (kg) vs. crown photo area (m^2).

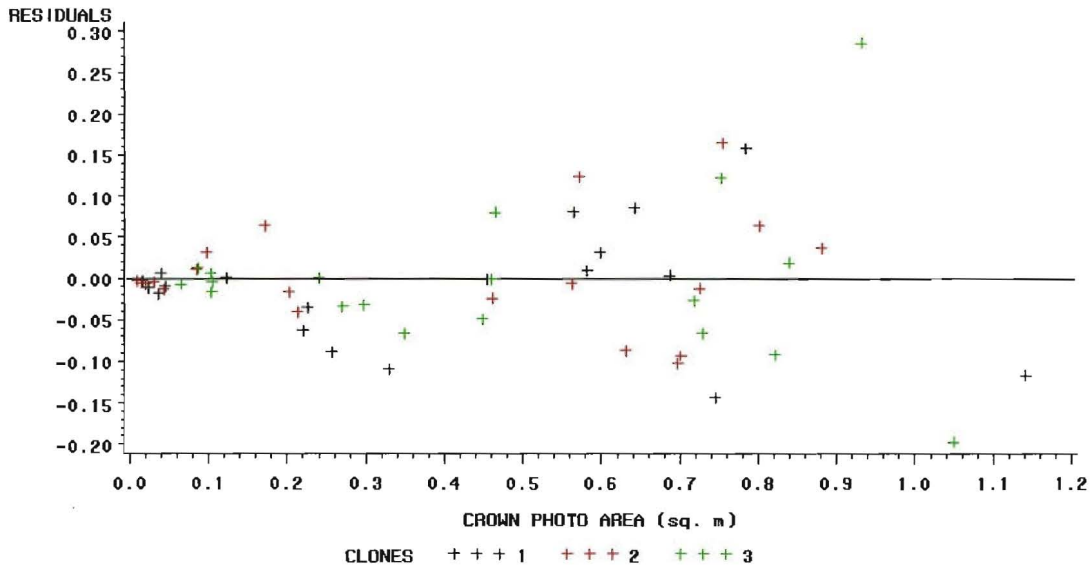

Figure 5.25: Plot of residuals by crown photo area (m^2).

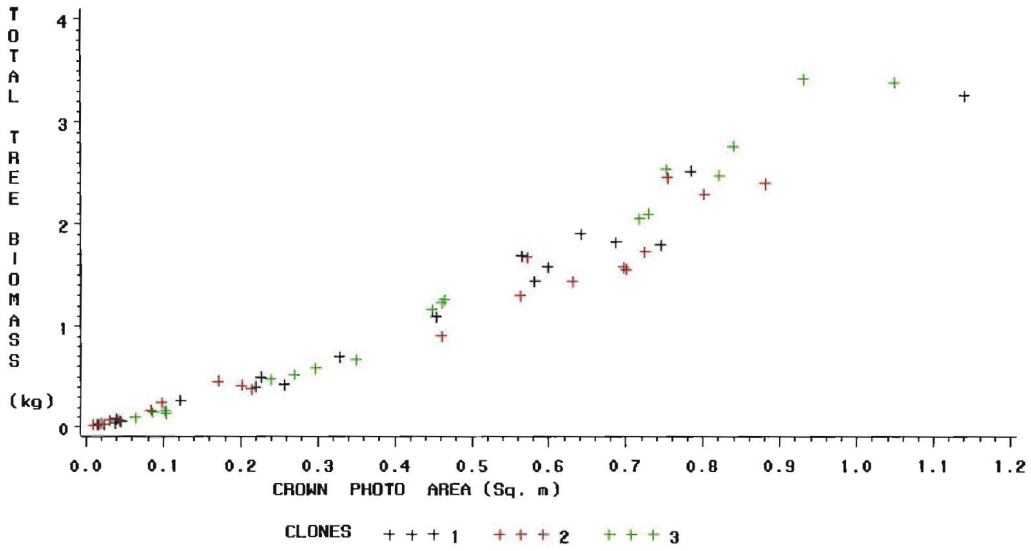

Figure 5.26: Relationship between total tree biomass (kg) and crown photo area (m^2)

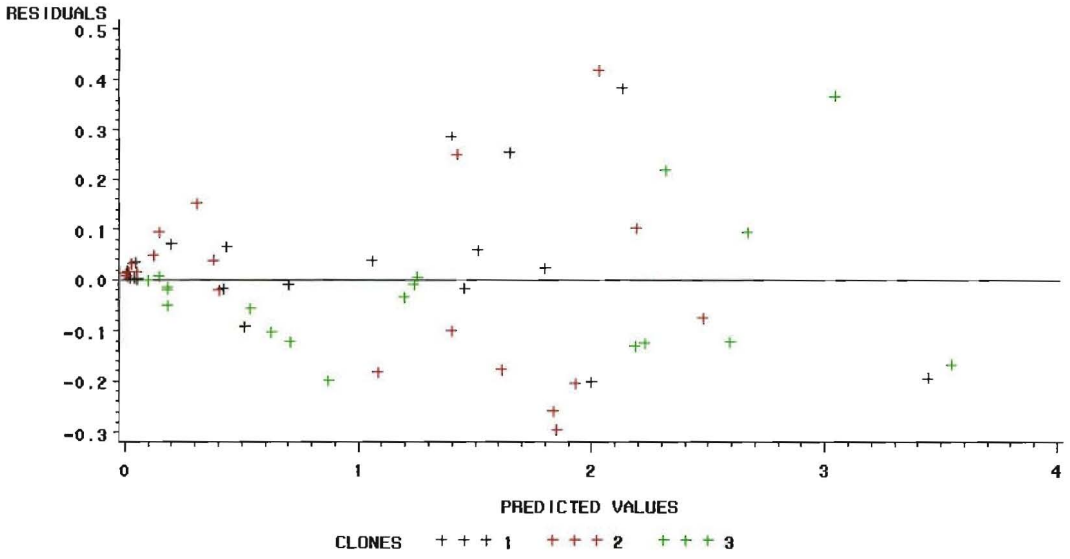

Figure 5.27: Plot of residuals by predicted total tree biomass (kg).

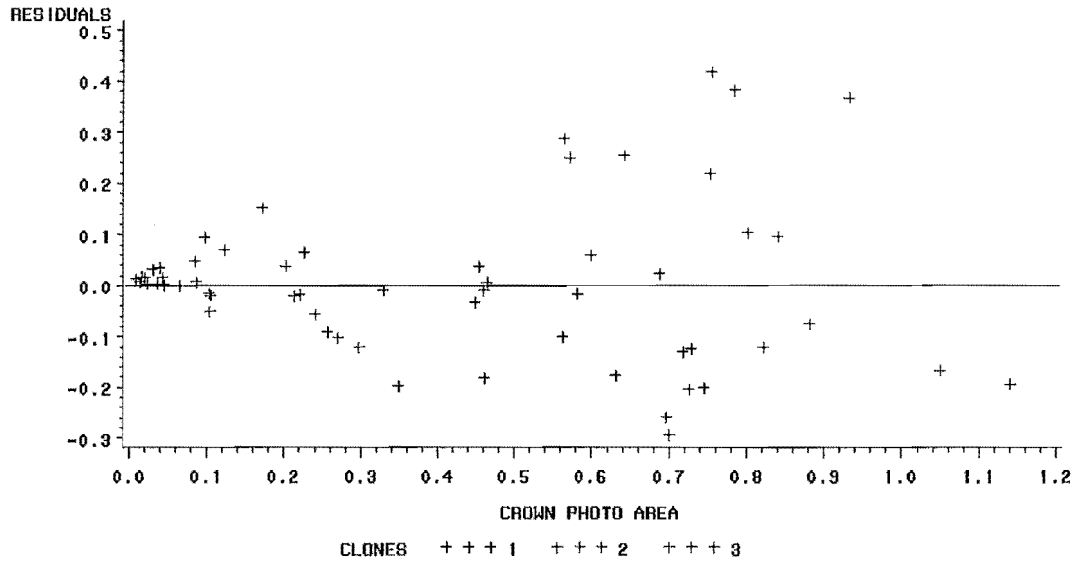

Figure 5.28: Plot of residuals by crown photo area (m^2)

The relationship between stem biomass and tree volume index (GLD^2*H), (Figure 5.29) was best described by an exponential function (equation 5.14). The fitted equation had different shape coefficient values for clones and weeding treatments. The final form of the equation used was;

$$Stem\ biomass = (\alpha_0 + \alpha_1 * V_1 + \alpha_2 * M_1) * (GLD^2 * H)^{(\beta_0)} \quad (5.15)$$

where;

α and β were regression coefficients and V_1 was a dummy variable for clone 1 while M_1 was a dummy variable for Wc0.75.

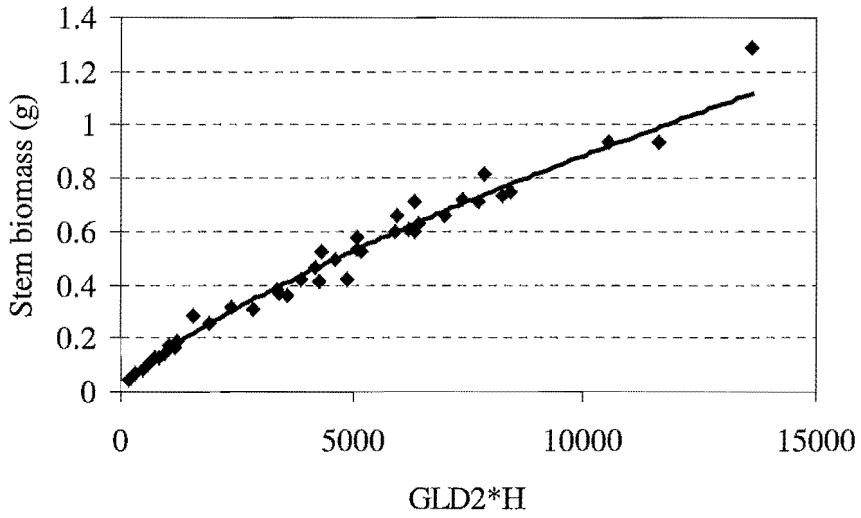

Figure 5.29: Relationship between GLD^2*H (cm^2) versus stem biomass (kg).

There were different rate coefficients for clones and weeding treatments as summarised in the model outputs in table 5.4. The residuals were between $^{-}0.1003$ and $^{+}0.0909$, (Figures 5.30 - 5.31). A linear model allowing for differences in intercepts and slopes for clones and weeding treatments was rejected due to its high residual root mean squares (table 5.4). The coefficient values were, $\alpha_0 = 0.0008477$, $\alpha_1 = -0.00002277$, $\alpha_2 = 0.00003757$ and $\beta = 0.75301$. Although the clone and weeding variables were significant, their absolute effects on the relationship between stem biomass and D^2*H were small.

Table 5.4: Model outputs for stem biomass versus GLD^2*H model.

Model	Residual MSE	Mean	Skewness	Kurtosis	Range of residuals
Linear model	0.0351	0	0.2582	3.9384	-0.1022 to +0.1118
Exponential model	0.00109	-0.00148	0.2182	2.5175	-0.1003 to +0.0909

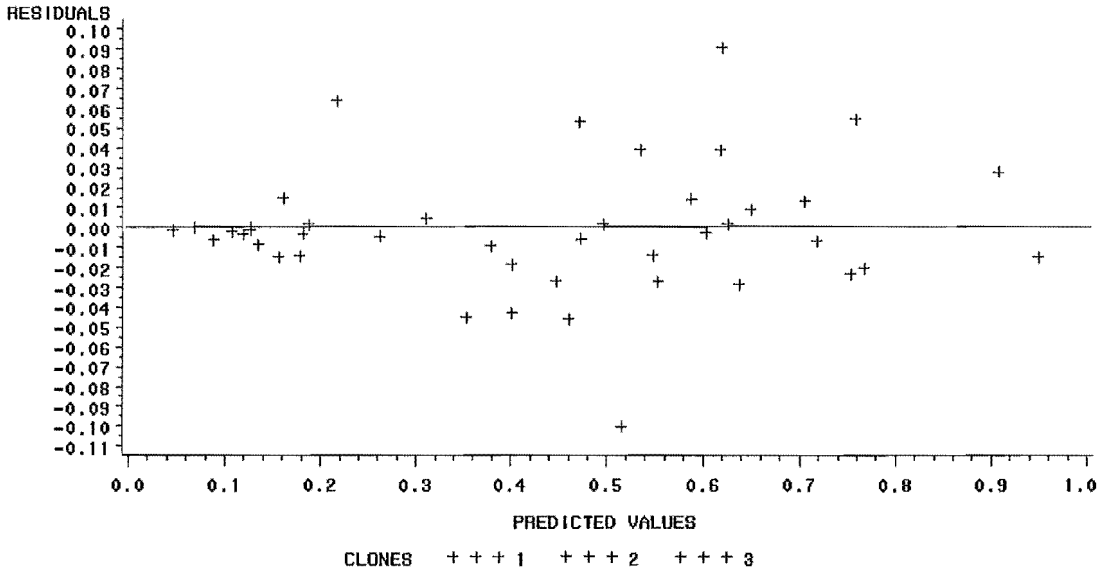

Figure 5.30: Plot of residuals versus predicted for stem biomass model.

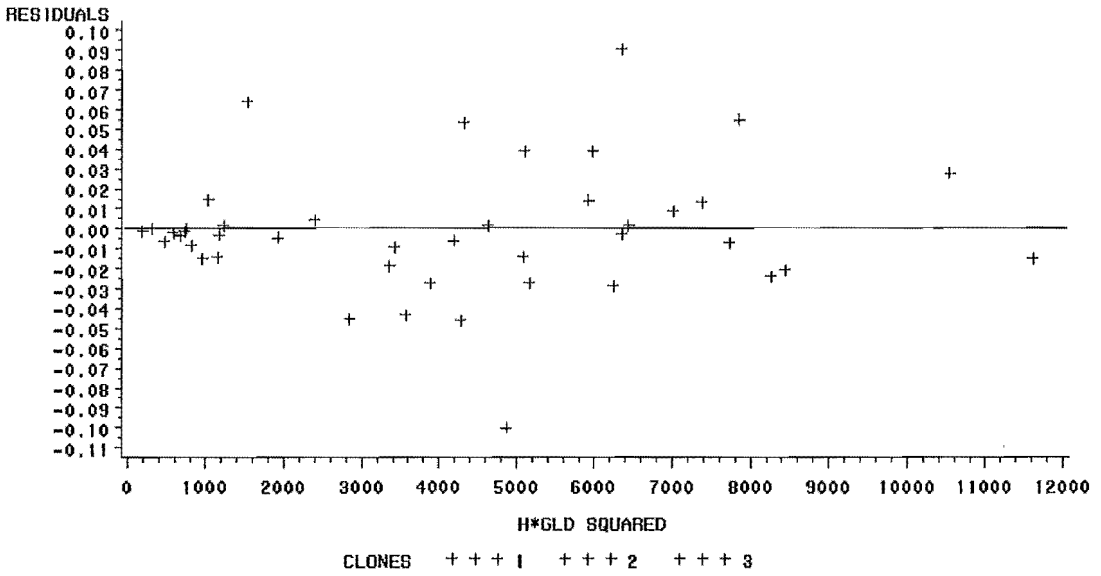

Figure 5.31: Plot of residuals versus GLD^2*H for stem biomass model.

A strong linear relationship existed between branch biomass and GLD^2*H (Figure 5.32). Branch biomass was modelled using a linear function, which allowed for changes in intercepts and slopes for clones and age effects. The fitted function was;

$$Branch \quad biomass = (\alpha_{i,j}) + (\beta_{i,j}) * (GLD^2 * H) \qquad (5.16)$$

where $\alpha_{I,j}$ and $\beta_{I,j}$ are intercepts and slopes for i^{th} clone and j^{th} age.

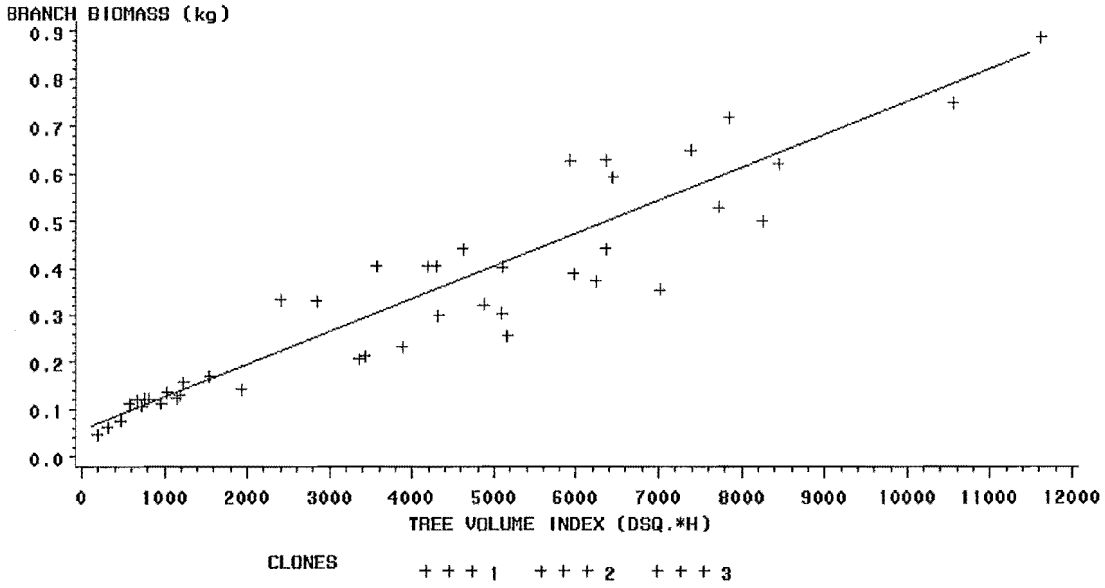

Figure 5.32: Relationship between Dsq.*H (= GLD^2*H) (cm^3) versus branch biomass (kg).

Clone 2 had a different intercept while age 2 had a different slope (see Table 5.5). The model R^2 was 0.895 with all residuals lying between -0.185 and +0.144. Plots of residuals displayed acceptable trends showing little bias (Figures 5.33 to 5.34).

Table 5.5: Model outputs for branch biomass versus GLD^2*H model.

Coefficient	Name or Dummy variable	Estimated value
α_0	default intercept	-0.035602
α_1	intercept for age = 2	0.07602
β_0	default slope	0.00007764
β_1	slope for age = 2	0.00007239

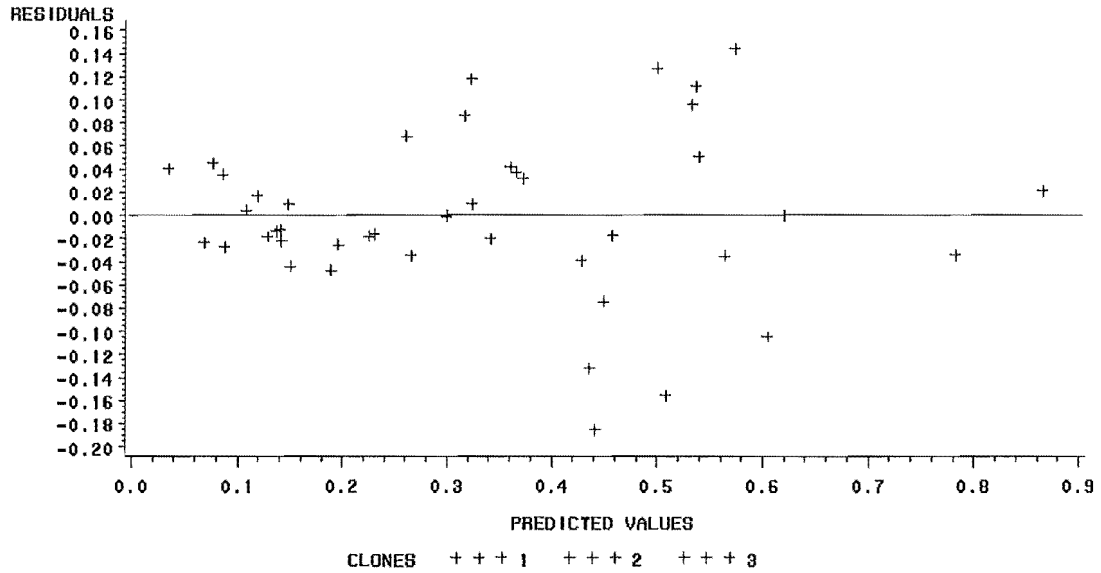

Figure 5.33: Plot of residuals by predicted branch biomass values.

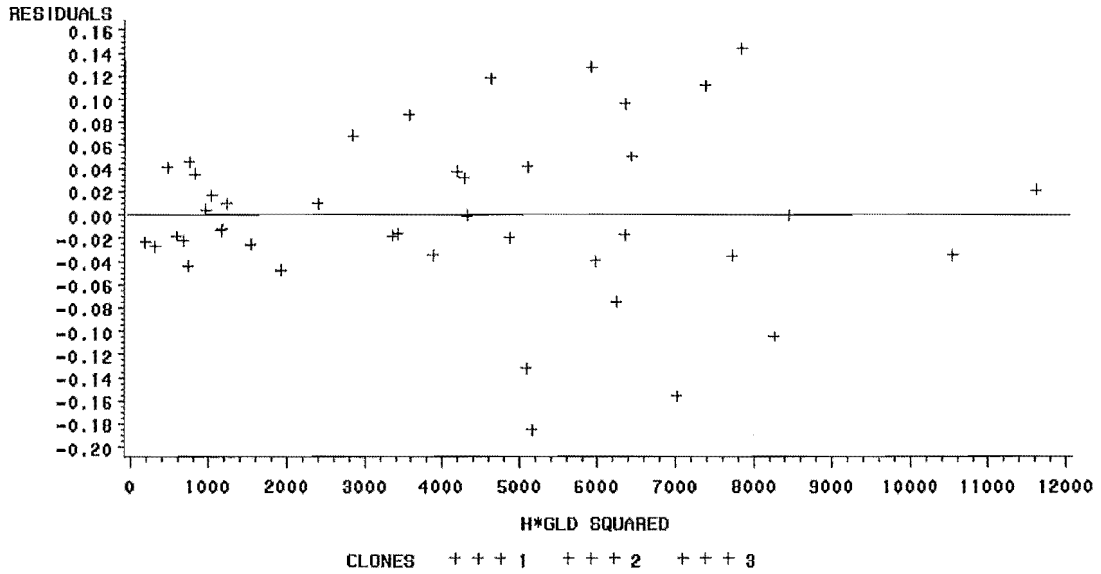

Figure 5.34: Plot of residuals versus GLD^2*H for branch biomass model.

Competition from weeds reduced crown photo areas drastically. In year 3 trees in weedy plots grew in crown photo areas by only 5%, 10% and 17% of those recorded by trees in the complete weeding, 2 m diameter spots and 1 m diameter spots respectively (Figure 5.35).

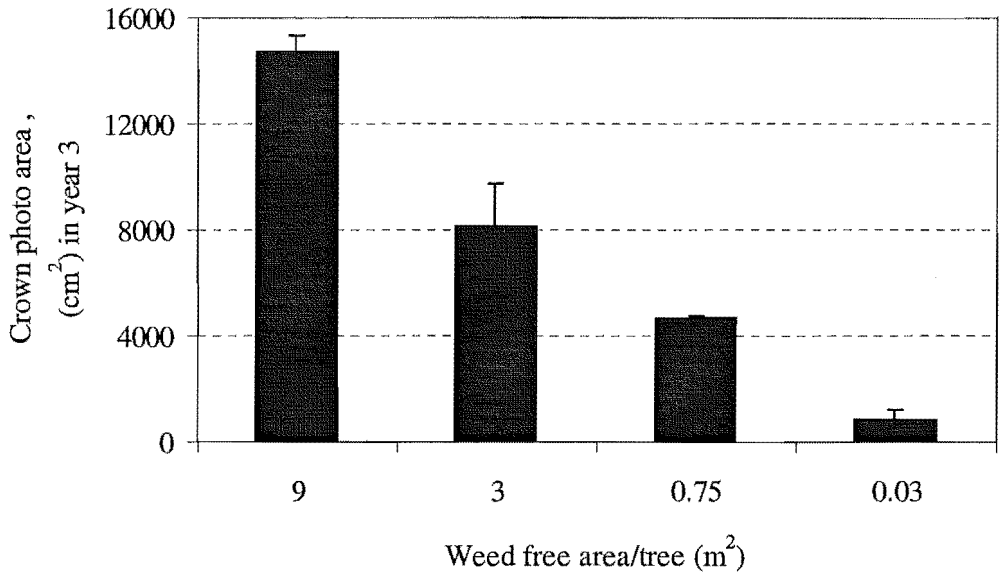

Figure 5.35: Mean crown photo area/tree growth in year 3 versus weed free spot size (m^2).

Response curves (Figure 5.36) fitted to data showed that the effects of increasing weed free area/tree on crown photo area growth in year 3 were best described using the equation;

$$Y = \alpha * X^{\beta} \qquad (5.17)$$

In all cases α and β were regression coefficients, *Y* represented crown photo area and *X* was weed free area per tree (m^2); α = 0.4961 and β = 0.4917.

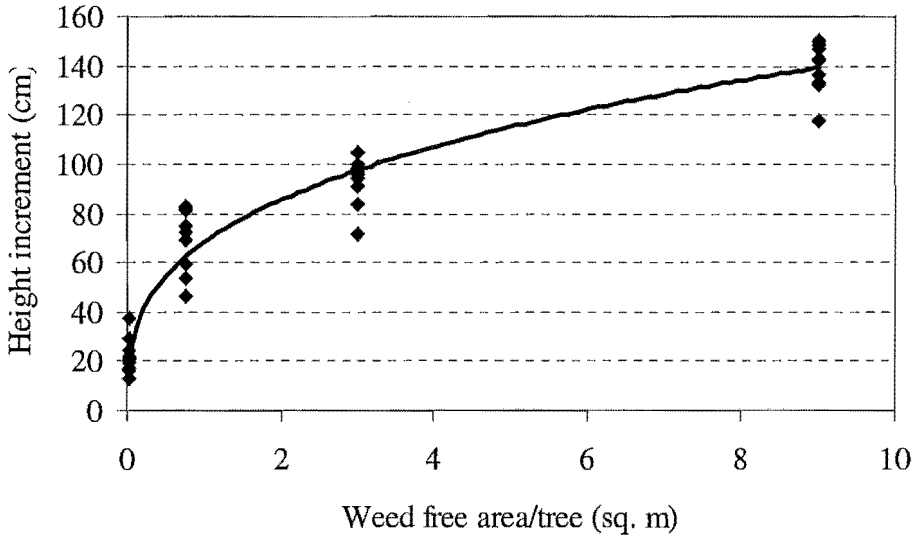

Figure 5.36: A response curve for 3-year-old radiata pine height growth (year 3) by weeding intensity.

The regression equations developed from limited destructive sampling for foliage dry weight (equation 5.13) and total tree above ground dry weight (equation 5.14) were used to estimate standing tree foliage weight and biomass (Figures 5.37 and 5.38).

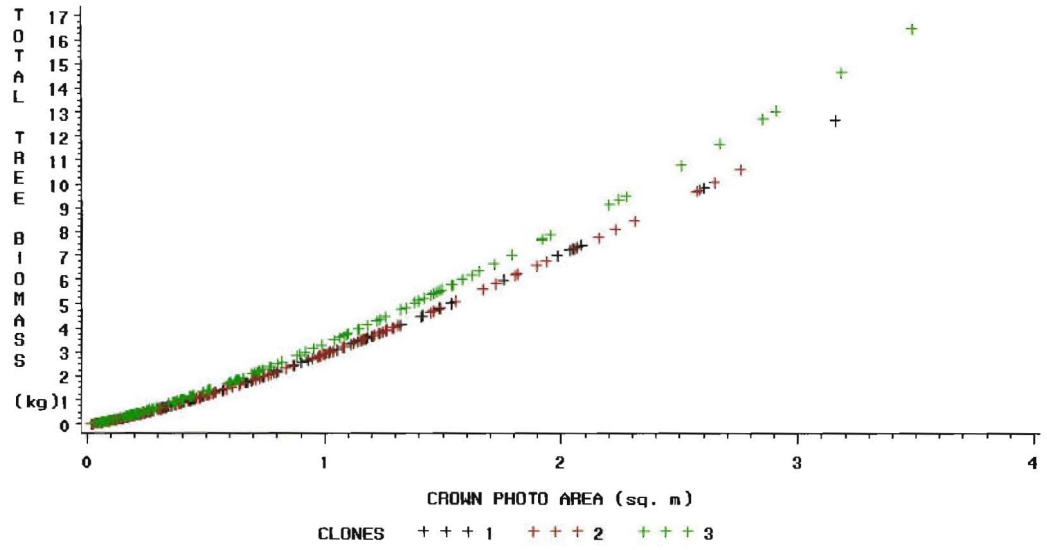

Figure 5.37: Predicted total tree biomass (kg) by crown photo area (m^2) for clone 3 (upper) and clones 1 and 2 (lower) at age 3 years.

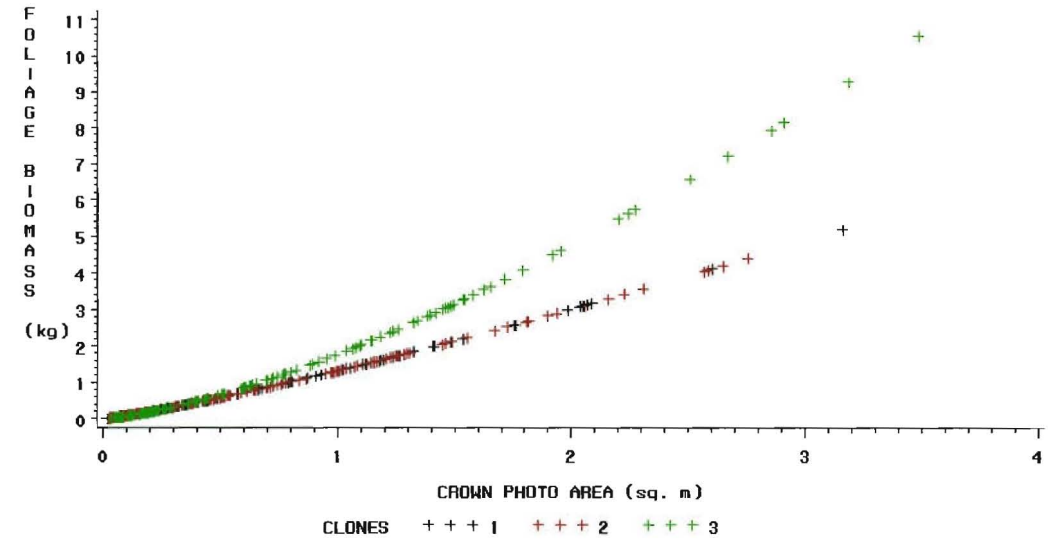

Figure 5.38: Predicted total tree foliage weight (kg) by crown photo area (m^2) for clone 3 (upper) and clones 1 and 2 (lower) at age 3 years.

The biomass of standing trees in Wc0.75 was also calculated by summing up the values (method 2) given by the stem weight versus GLD^2*H (equation 5.14), branch weight versus GLD^2*H (equation 5.15) and foliage weight vs. crown photo area (equation 5.12). The outputs were compared to those from total tree biomass versus

crown photo area (method 1, equation 5.13). The models (methods 1 and 2) were also used to estimate standing tree biomass for trees in Wc9. The results showed that method 2 gave lower biomass values compared to method 1 (Figures 5.39 and 5.40, also table 5.6).

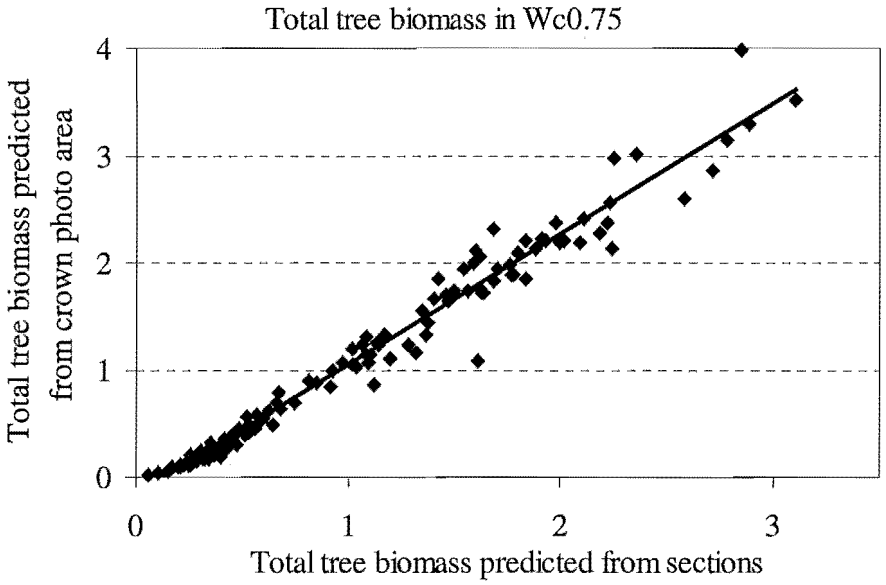

Figure 5.39: Relationship between total tree biomass using summation of sectional biomass and using crown photo areas for Wc0.75.

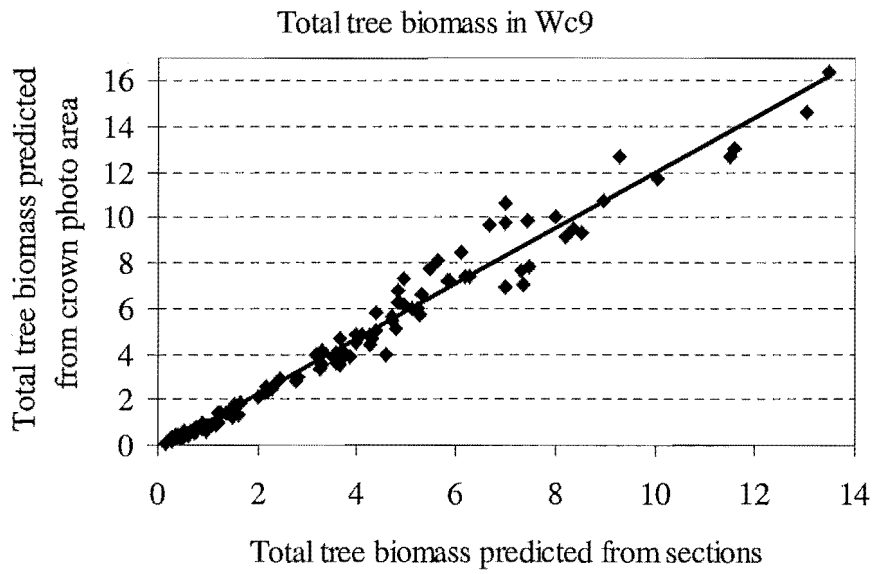

Figure 5.40: Relationship between total tree biomass using summation of sectional biomass and using crown photo areas for Wc9.

Further, the arithmetic mean tree biomass values at age 3 years for the standing trees in the experiment were compared for crown photo areas (method 1), and summing up sectional biomass (method 2). Average foliage dry weight per tree was also calculated. Weeding treatments Wc0.75 and Wc9 were used for this exercise. The tree means of the destructively sampled trees were also calculated (Table 5.6).

Table 5.6: Average total tree biomass and foliage weight of pooled data using method 1 and method 2 and compared to actual measured values (* shows actual values of trees that had 2 m spots only during the 3rd growing season).

Weeding	Mean tree Biomass (kg)			Mean foliage weight (kg)	
treatment (s)	Method 1	Method 2	Actual wt.	Model	Actual wt.
Wc0.75	1.77	1.59	1.75	0.87	0.87
Wc3 (1 year)*	-	-	2.26*	-	1.08*
Wc9	6.6	5.59	-	3.26	-

5.4 DISCUSSION

The deleterious effects of weeds on tree growth have been discussed by many researchers (e.g. Walstad and Kuch 1987, Evans 1992, Richardson 1993, Nambiar and Sands 1993, Perry *et al.* 1993, Zedaker *et al.* 1993, Sands and Nambiar 1984, Wagner and Radosevich 1991a, Kirongo 1996, Willoughby 1999). In sites with low rainfall, such as Canterbury, weeds need to be controlled promptly to avoid massive crop failures. Some researchers have reported competition from weeds to have greater effects on diameter than height increment (e.g. Benson *et al.* 1992, Kirongo 1996). In this study, crown photo areas (leaf areas) were most severely affected by competing vegetation. Third-year crown photo area increment of trees in the control were reduced by 95% compared to trees in complete weeding (Figure 5.35). This effect on canopy was due to delayed needle initiation and reduced needle elongation, and therefore less light interception area.

Trees growing with weeds suffered 5 detrimental effects:

1) moisture deprivation;
2) delayed needle emergence and therefore, a shorter growing season;
3) poor leaf area growth and chlorotic older foliage (hence trees with small crowns);
4) reduced amounts of new foliage; and
5) increased retention of older (3-year-old), less efficient foliage (Chapter 5 part II).

All these factors reduced the trees' growth potential and ultimately reduced height and GLD growth. Similar observations have been reported by other researchers (Zutter *et al.* 1996, Raison *et al.* 1992a,b, Benson *et al.* 1992, Kirongo *et al.* (in prep.). Brix (1983) and Raison *et al.* (1992b) concur that the production and ample development of new foliage is a major factor influencing canopy development and consequently, tree height and diameter growth. Reduced leaf area (poor growth, leaf chlorosis) implied that trees in the unweeded control had fewer chlorophyll reaction sites available for photosynthesis. This and other factors mentioned earlier may explain, in part, why trees growing with weeds were predestined to perform poorly in the future.

Soil moisture measurements in Wc9 and Wc0.03 showed reduced moisture levels from depths of 20 cm downwards in the weedy plots (Kirongo *et al.* (in prep). Trees in these plots must have suffered reduced needle water potential (Sands and Nambiar 1984) and reduced photosynthetic capacity due to low conductance or closed stomata counteracting the effects of dehydration. Acute soil moisture shortages can also affect soil aeration and strength resulting in poor root growth (Sands *et al.* 2000). These observations are supported by Zutter *et al.* (1999b) who found reduced fine root density and growth (top 15 cm of the soil) of loblolly pine growing with weeds. Benson *et al.* (1992) reported water stress to result in stem shrinkage in radiata pine. Meanwhile, Raison *et al.* (1992b) reported that water stress reduced final needle length and time to full elongation in 10-14 year old radiata pine in Australia. Water stress can lead to reduced photosynthesis (Rook *et al.* (1987), inhibition of primordia initiation (Bollmann *et al.* 1986) and ultimately affect canopy development (Brix 1983, Raison *et al.* 1992a). Consequently, subject trees may suffer reduced photosynthetic activity (Landsberg 1986).

Water stress also affects cell division and expansion and may indirectly interfere with processes which lead to provision of metabolites to new vigorously growing foliage (Dale 1982) resulting in reduced LA expansion. In the short term, trees use mechanical means e.g. reducing stomatal aperture to counteract water stress. But in the long term, foliage growth and carbohydrate partitioning are affected (Landsberg 1986). This latter observation is in accord with the observed crown areas and needle growth trends in this study. The water stressed trees may have allocated more to below ground resources, a factor which was not addressed in this study.

Foliage growth dynamics showed that fascicle LAs differed significantly in different crown parts. This is in agreement with observations by others (Watts *et al.* 1976, Beadle *et al.* 1985, Grace *et al.* 1987b). It was observed that needles in the upper part of the crown had higher LA values than needles in the lower crown (data not shown). This may be due to differences in light attenuation resulting in low light levels in crown parts at the bottom of the tree. Watts *et al.* (1976) observed low light levels in the bottom part of the crown of Sitka spruce which they correlated with lower growth of needles.

Needle growth trends at this site were quite different to those described in other similar studies for radiata pine, notably Rook *et al.* (1987) and Bandara (1997). The logistic growth curves fitted to needle growth data by the above named researchers implied that needles grew very slowly at first followed by a period of very fast linear phase (with a steep slope) and then decelerated to an upper limit towards the end of the growing season. However, in this study needles grew at much slower rates especially from November to February (New Zealand mid-summer) when moisture stress was at its highest. This affected the rate and shape coefficients as well as the final maximum lengths attained (Figure 5.41). For example, maximum lengths of fully expanded 1-year old needles were only 14 cm compared to 17 cm in other studies (e.g. Rook *et al.* 1987, Snowdon and Benson 1992).

Significant differences in needle elongation, crown photo areas, SLA, height and diameter (chapter 4) growths were reported between clones. Bollman and Sweet (1976, 1979) and Bollmann *et al.* (1986) reported drought to affect rate of needle

formation in some clones, and site differences to influence primordia initiation and shoot elongation.

Above ground allocation patterns varied with tree age, as well as among clones. Different clones had different growth and above ground allocation strategies (clones 1 and 2 versus clone 3 - Figures 5.37 - 5.38). These differences were partly responsible for the observed differences in height and diameter growth. Family differences in above ground allocation have been reported in similar studies (e.g. Snowdon 1985, Snowdon and Waring 1985). This study showed that juvenile trees (up to 3 years old) allocated increasingly more biomass to branches (Figure 5.20) and especially to foliage. Allocating more to branches is important to develop an elaborate crown structure on which foliage would be held.

The proportions of biomass allocated to foliage were different to those reported for older trees with closed canopy or without moisture stress (e.g. Rook *et al.* 1987). For example, Beets and Whitehead (1996) reported allocation to stems to be 63 % to 67 % between tree age 7 to 17 years. Meanwhile, allocation to foliage and branches decreased from 23 to 21 % and 12 to 8 % respectively. Snowdon and Waring (1985) reported branch to stem ratios to vary between 0.215 to 0.505 in 4 year-old radiata pine cuttings. In this study the ratio of biomass allocation of branch to stem decreased from 4 in year 1 to 0.67 by year 3.

Dunsandel is a dry stony site and that had serious effects on moisture availability and possibly root growth. Trees in Dunsandel may be expected to be conservative; not growing extravagantly as may be expected in sites with unlimited moisture resources. Root growth was severely limited below the rip depth with most roots growing along the rip line (Figure 5.42). Due to the dry nature of the site competition for below ground resources especially moisture may influence below ground allocation significantly. This study concentrated on above ground allocation only. There is definitely a need therefore to carry out further studies under similar treatments on below ground allocation patterns.

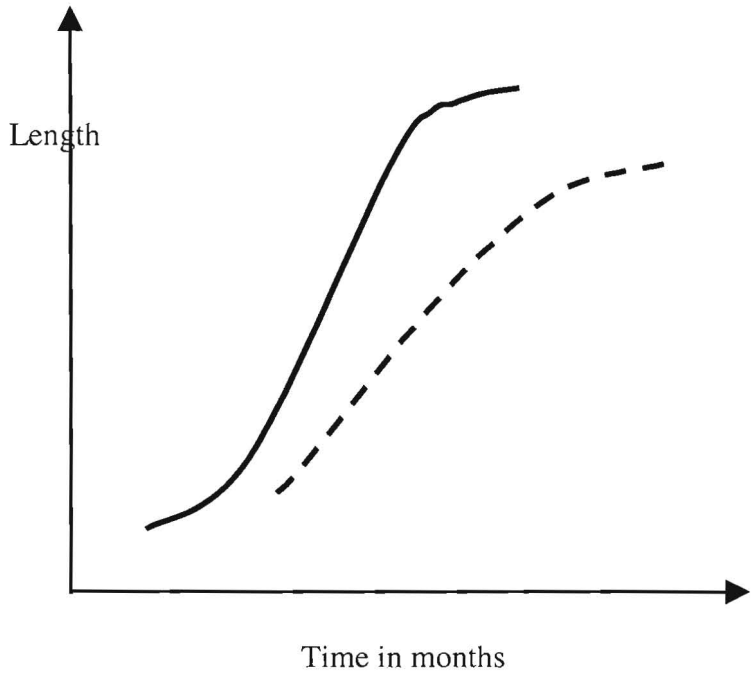

Figure 5.41: The general hypothesised form of needle growth trends of Dunsandel study (broken line) compared to those described by logistic fits (solid line) e.g. Rook *et al.* (1987).

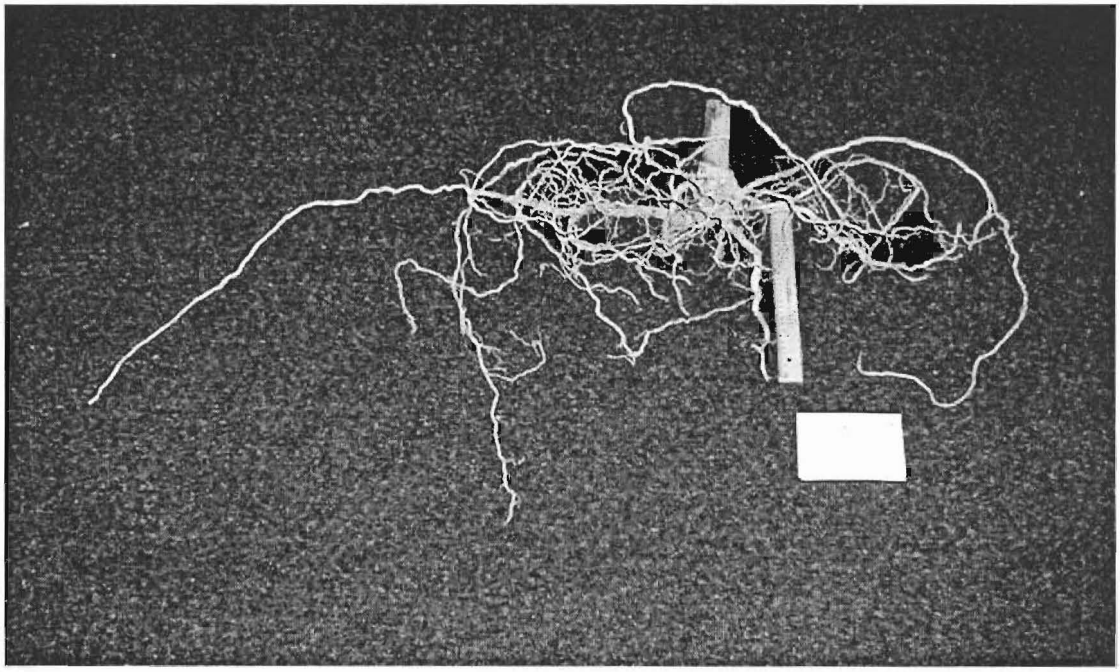

Figure 5.42: A photograph of roots of a representative tree from Wc0.75 showing an effective root depth of about 30 cm (the rule on the photo) with most large roots running left-right along the rip line.

Biomass estimates given by method 2 (summation of parts) were found to under predict branch and stem weight. This raised concerns about the use of method 2 to estimate standing tree biomass in other treatments (e.g. Wc3 or Wc9). Given that foliage weight was estimated using the same function (equation 5.13) the discrepancies were due to poor estimates of stem and branch wood. Due to differences in proportional allocations of trees growing in other micro-environments (not Wc0.75), these errors could be considerable (Baker *et al.* 1984). The foliage dry weight estimates from equation 5.13 were comparable to those of radiata pine of similar age reported elsewhere (e.g. Beets and Pollock 1987).

Beets and Pollock (1987) reported leaf weight of between 0.48 to 1.40 kg, depending on the site, for 3-year old radiata pine at Puruki in the North Island of New Zealand. The results from this study are within the range of these estimates (0.89 - 1.48 kg). Total tree biomass at age 3 years, for the trees by Beets and Pollock (1987), varied between 1.43 - 3.57 kg for the poor and better site. The results in this study are in agreement, but highlight the massive benefits of complete weeding over 1 m spots (1.43 - 2.00 kg for Wc0.75 and 2.01 - 3.01 kg for Wc3, see Table 5.3 section 5.3.3.1). The ratios of foliage to total tree biomass in this study (44 - 52 %) were slightly higher than those reported by Beets and Pollock (1987) (34 - 48 %) for 3-year old radiata pine. Higher readings in this study may be due to the use of improved genotypes and/or wider spacing. The stocking levels used by Beets and Pollock (1987) were twice those used in this experiment. Given that Puruki has more rainfall it is possible that trees may compete very early at close spacing. This is a conjecture, however.

Calculating total tree biomass by summing the values of stem, branch and foliage sections led to under prediction. Individual tree values were in error by up to 30 % (one value 48 %). This was not surprising given that the equations used to estimate allocation to stem and especially branch biomass were developed from trees which had 1 m diameter spots (Wc0.75) of weed control. The allocation patterns of these trees were evidently different from those growing under total weeding, for example. This was obvious from the plots of proportional allocation (Figures 5.20 section 5.3.3.1) which showed that harvested trees that had 2 m diameter spots in the third

year had already developed different above ground allocation patterns compared to those still in 1 m diameter spots.

The use of generalised equations or those developed from trees growing in different environments has raised concerns before (e.g. Snowdon and waring 1985, Snowdon 1985, Baker *et al.* 1984, Madgwick 1994). Snowdon and Waring (1985) reported significant family differences in branch wood to stem ratios. Snowdon (1985) found genetic effects to be the dominant factor leading to bias. He reported differences of up to 29 % if equations developed from one family were used for another family. Meanwhile Baker *et al.* (1984) reported site and treatment differences to be the major causes of bias. It is therefore, recommended that equations developed from trees growing under 1 m spots be used cautiously. The use of crown photo areas to estimate foliage dry weights for the whole experiment should also be done with care. This is because the relationships may not hold for trees growing in different weeding treatments.

Theoretically, total tree biomass estimates from the summation of parts should give more accurate results. However, it is important that the equations be developed from trees of similar age, genotype and growing in similar micro-environments to avoid significant bias in estimates. As this study showed, increasing spots size diameters from 1 to 2 m during the second year resulted in differences in above ground allocation at the end of the third year.

In this study crown image areas were better predictor variables of total above ground tree biomass and foliage than GLD or volume index (GLD^2*H) (data not shown). Other reasons for preferring crown photo areas to GLD or volume index were: 1) using stem (i.e. GLD or volume index) to estimate canopy and then growth and then allocation and back to stem and canopy is circular (i.e. stem => canopy => growth => allocation => stem => canopy); and 2) stem measurements are less sensitive to seasonal changes in resource pools. For these reasons crown area photographs were preferred.

5.5 CONCLUSIONS

Controlling weeds during the main growing season improved current tree growth and ensured that crop trees were morphologically and physiologically better prepared to take full advantage of future favourable growing conditions.

The presence of weeds in the same micro-sites as crop trees had 5 detrimental effects:

1) moisture deprivation;
2) delayed needle emergence and therefore, a shorter growing season;
3) poor leaf area development leading to trees with small crowns;
4) less new foliage and chlorotic older foliage, reducing the effective photosynthetic area; and
5) increased retention of older (3-year-old), less efficient foliage (Chapter 5 part II). These factors led to reduced height and GLD growth.

Crown photo area (= leaf area) was more affected by the presence of weeds than height or GLD.

Moisture was the major factor exacerbating the competition effects through its effects on needle development and crown structure.

Clone 3 was better suited to this site by year 3 than the other 2 clones studied.

Above ground tree biomass estimated from the summation of sectional biomass was lower than estimates made from crown photo areas, especially for trees not growing in Wc0.75. It is recommended that equations be used for trees growing in similar micro-environments (and genotype) to avoid excessive bias in estimates.

PART 2: MODELLING THE MORTALITY OF NEEDLES WITHIN CROWNS OF 3-YEAR OLD RADIATA PINE CLONES

5.1 INTRODUCTION

Needles in the canopy may die because of physiological aging, self-shading and/or stress (water, space, light) (Dale 1982). The quantitative estimate of needle mortality by crown position and leaf age classes is an important variable in models of canopy leaf area balance. Realistic models of canopy processes must have accurate and reliable predictions of not only leaf area (LA) additions but also the losses as a result of natural and/or induced senescence (e.g. competition, defoliation, browsing), (Kinerson *et al.* 1974, Landsberg 1986). Rook *et al.* (1987) developed models of foliage development within the crowns of 7- and 9-year old radiata pine stands growing in stress-free environments in the North Island of New Zealand. However, needle mortality was subjectively assessed resulting in biased estimates, to which Rook *et al.* (1987) concede:

"...but the values of winter leaf abscission in the literature are too uncertain to allow reliable estimates of net changes in foliage...."

Other researchers have used needle fall (litter fall) figures to estimate losses in LA from tree crowns (e.g. Kinerson *et al.* 1974, Pook 1984, Dalla-Tea and Jokela 1991, Raison *et al.* 1992a). However, needle fall underestimates the actual losses in functional LA or needle abscission (Raison *et al.* 1992a). This is because dead needles can remain on the trees for up to a whole season. For example, Raison *et al.* (1992a) report that 30 to 50 percent of senescent needles were still on the crowns of 10-14-year-old radiata pine trees. What is more, the litter needles lack identity and may have come from any position in the canopy. Furthermore, loss in mass of the dead needles due to leaching and decomposition compounds the problem even

further. This implies that using leaf weight of litter needles to estimate LA will result in biased estimates.

While big strides have been made especially in modelling the production and elongation of current season's foliage in a growing season (e.g. Kinerson *et al.* 1974, Rook *et al.* 1987, Raison *et al.* 1992b), the general area of modelling needle mortality (actual losses of leaf area) as a function of needle age, crown position and time as practiced in the study described here is a new development. Moreover, most of the studies in the literature dealt with mature stands or those over 5 years of age. The processes of such stands are markedly different from those of juvenile crops because:

1) juvenile crops have not reached the inflection point and are growing exponentially (Mason 1992);
2) juvenile crops have not closed canopy and may have less within crown shading. Thus their within canopy processes (temperature regimes, water vapour, light conditions - Landsberg 1986) will be markedly different from those of older crops; and
3) juvenile crops have proportionally higher amounts of physiologically young foliage compared to older crops which have a 'steady' state (Kinerson *et al.* 1974) of foliage age classes.

The question of genetics is also an important one and models of canopy processes need to address this as well. Different genotypes have been reported to exhibit differences in growth characteristics (Bollmann and Sweet 1976, 1979, Madgwick 1983b, Snowdon and Waring 1985, Bollmann *et al.* 1986, Theodorou *et al.* 1991). In addition, models of canopy processes should be sensitive to cultural treatments (e.g. weed competition gradients) if they are to be of immediate value to managers and other tree growers. Part of the research in this thesis aimed to address these concerns.

5.1.1 Theory

Needles in the canopy may die because of physiological aging, shading and/or stress (Dale 1982). Mortality of needles in juvenile crowns has two main components; losses from the stem and losses from the branches. In trees, the quantity and quality of usable solar energy reaching the needles reduces with crown depth (Charles-Edwards *et al.* 1986, Grace *et al.* 1987a, Xu 2000). Fascicle mortality was therefore hypothesised to be a function of the following variables:

$$Mortality = f(Trt, Cl, Nedage, Tree\ ht, Locatn, Crown) \quad (5.17)$$

where;

Trt = weeding treatment,

Cl = clone,

Nedage = needle age,

Locatn = stem or branch,

Tree ht = height variables,

Crown = crown characteristics.

Height variables used were; 1) height from the top to the sampling unit, 2) proportional height and 3) average height between T_1 and T_2 (start and end of the study period). Crown variables used were; 1) crown area at the start and end of the period, 2) distance from the outside edge of the crown to the sampling unit, 3) number of whorls at T_1 and T_2, 4) average number of whorls between T_1 and T_2, 5) number of whorls above the sampling unit, and 6) crown width.

5.1.2 Some important considerations in choosing formulations

Given that tree crowns are heterogeneous in structure and the environment within them is not uniform even for short time periods, it is important that the formulations used portray this fact. Thus only equations which are theoretically plausible and make practical sense should be used. For example, two trees with seemingly similar

canopies may have significantly different within crown environments if they differ in their crown shape, branch architecture and morphology and leaf area density. These considerations were taken into account when formulating expressions of needle mortality. Any expressions which did not make biological sense were avoided.

5.1.3 Terms and definitions

C = fully expanded current season foliage which is age 0 before winter (May-September) of the year formed.

C+1 = one year old foliage at the start of the new growing season.

C+2 = two year old foliage at the start of the new growing season.

C+n = n year old foliage at the start of the new growing season.

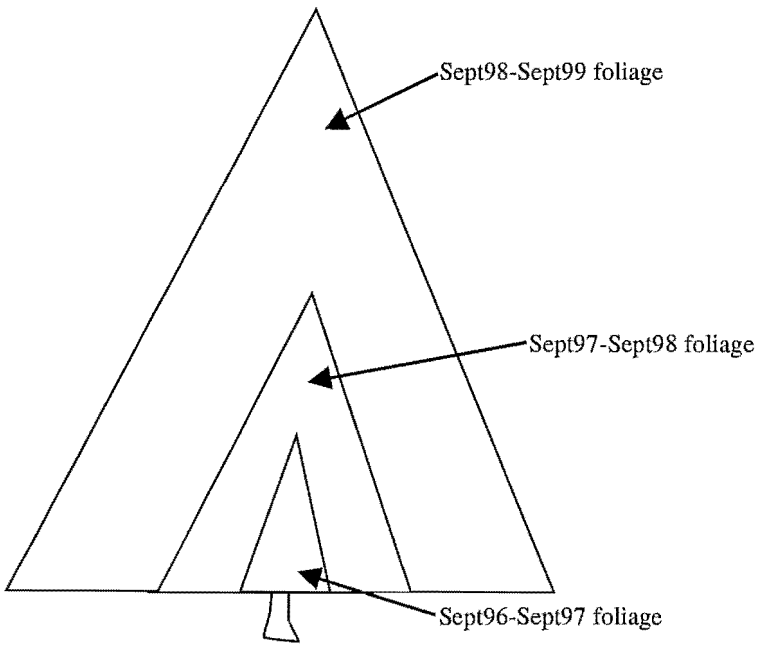

Figure 5.43: Hypothetical needle arrangement by season of emergence within the crown of a 3-year-old radiata pine tree.

5.2 STUDY METHODOLOGY

In September 1997, 72 (two trees per clone, per weeding treatment per replicate) trees were selected systematically to include a range of tree sizes. Needle mortality sampling units were marked on all fully expanded one-year-old (C+1) foliage between branch whorls on the stem and along branches. In the winter of 1998, the old sampling units, (C+2) (see below) were assessed by counting the number of surviving needles. New sampling units were placed in all new (C+1 = 1998-1999 season) foliage. In the winter of 1999, all the sampling units were re-assessed by counting the number of 3-year-old (C+3) and 2-year-old (C+2) needles remaining in the sampling units.

Sampling units varied in length along a branch or stem from 2 cm to 10 cm depending on tree size and position in the crown. The allocation of sampling units to crown positions was systematic within the stem and branch sections. The aim was to have each stem section between branch whorls and all branch orders and segments represented in the sample. However, within a growth segment the sampling units were randomly allocated to any position.

Mean 3-year-old needle mortality for the tree was calculated by weighting branch and stem mortality by their respective allocation proportions (data not shown). Thus mean tree needle mortality was given by;

$$\begin{aligned} \textit{Mean needle mortality} = {} & 0.35 * \textit{Stem mortality} + \\ & 0.65 * \textit{Branch mortality} \end{aligned} \qquad (5.18)$$

where 0.35 and 0.65 were the proportions of 3-year-old needles held in the stem and branches respectively.

Plots of mortality versus measured tree variables were plotted in GPLOT (SAS/STATS 1996). Linear regression procedures (SAS/STATS 1996) were used to identify significant variables related to needle mortality. Preliminary analyses showed that mortality from the branches was different from that in the stems. Two models of the general form shown below were therefore fitted.

$$Mortality = f(Trt, CL, Nedage, Tree\,ht, Locatn, Crown)$$

(equation 5.17 section 5.1.1, variables names are as described earlier).

5.3 RESULTS

Very few needles (<16 % in most plots) died during the first period (tree age 1-2, needle age = 2). Regression procedures (SAS/STATS 1996) showed that clones ($p < 0.0004$) and weeding-by-genotype interaction ($p < 0.0160$) were important variables influencing needle mortality from the branches. Needle fascicle deaths from the stem section for the same period were significantly influenced by weeding treatments ($p < 0.0001$) and proportional height ($p < 0.0179$). The interaction between blocking and weeding treatments was significant ($p < 0.003$) for both stem and branch needle mortality. Trees in weedy plots had significantly higher proportions of dead needles than trees in the other weeding treatments during the same period (Figure 5.44). Moreover, most deaths were from branches.

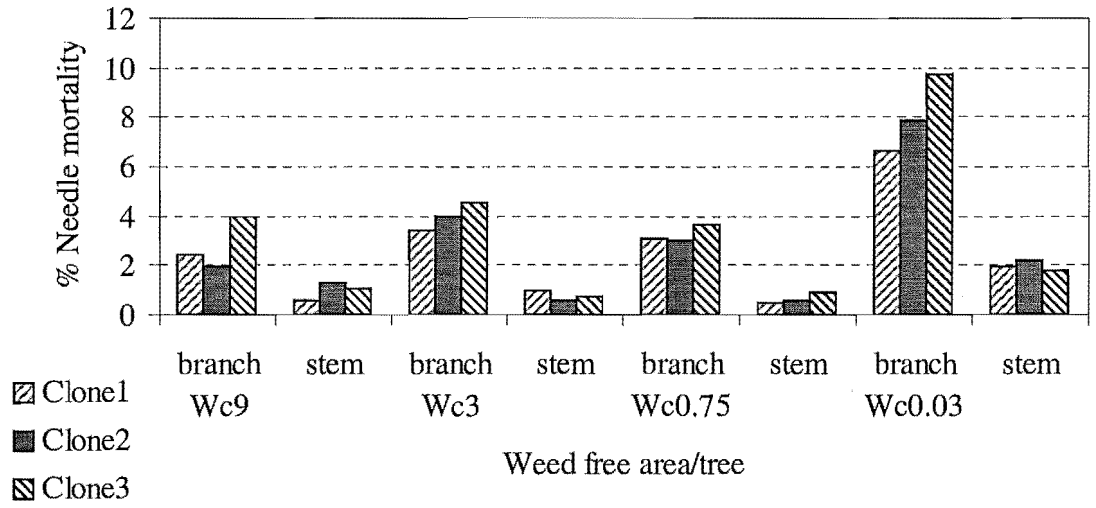

Figure 5.44: Fascicle mortality during the first period, tree age 2 and needle age 2.

During the second assessment (second period, tree age 3 years) it was observed that three-year-old needles had died *en masse* (Figure 5.45), especially those on the stems of trees in weeded treatments. Needles in other age classes were not affected (no

mortality recorded). Mortality of three-year-old needles from the branches was significantly influenced by blocking ($p < 0.0001$), clones ($p < 0.0001$), weeding-by-clone interaction ($p < 0.0001$), initial crown photo area (= estimates of initial tree foliage) ($p < 0.0009$) and mean crown area ($p < 0.0444$). Needle mortality from the stems in year 3 was influenced by proportional height ($p < 0.0004$), mean height ($p < 0.0001$), relative crown photo area ($p < 0.0199$), Mean branch whorls ($p < 0.0001$) and initial number of whorls ($p < 0.0367$).

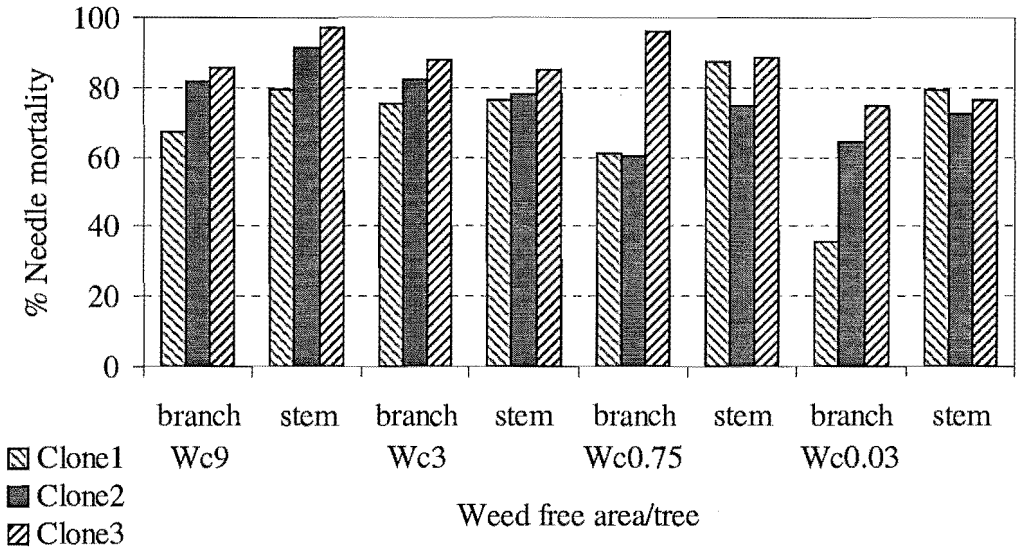

Figure 5.45: Fascicle mortality during the second period (tree age 3).

A general model of needle mortality by needle age and position (stem and branch) showed that mortality of 2-year-old needles (period 1) from the branches were influenced by genotype ($p < 0.0004$) and weeding-by-genotype interaction ($p < 0.0160$). At the same time, needle death from the stem was related significantly to weeding treatments ($p < 0.0001$) and proportional height ($p < 0.0179$). Proportional height was calculated as the ratio of height above ground to height at the end of the period.

For period 2 (needle age = 3 years) mortality from branches were related to genotype ($p < 0.0001$), genotype-by-weeding interaction ($p < 0.0091$), crown area at the start

of the period ($p < 0.0009$) and relative crown area ($p < 0.0444$). Relative crown area was calculated as the ratio of crown area growth during the period to the crown area at the beginning of the period.

3-year-old needle mortality from the stem for the same period was significantly related to proportional height ($p < 0.0004$), mean number of whorls during the period (whorls at T_1 + whorls at T_2 divided by 2) ($p < 0.0001$), mean height during the period (height at T_1 + height at T_2 divided by 2) ($p < 0.0001$), number of whorls above the plot at the beginning of the period ($p < 0.0367$), relative crown area growth ($p < 0.0199$) and crown area at the end of the period ($p < 0.0001$).

The final equations describing needle mortality in 3-year-old trees were;

$$Mort_{St} = 127.031 - 1.1065 * Pcht + 7.521 * Avwhl + 0.00323 * CA_2 - 0.0311 * \mathrm{Re}lCA - 0.499 * Avht \qquad (5.19)$$

$$Mort_{Br} = 25.369 + 18.9820 * CL - 1.458 * CL * Wc + 0.00953 * CA_1 + 0.05044 * \mathrm{Re}lCA \qquad (5.20)$$

where;

$Mort_{St}$ and $Mort_{Br}$ = stem and branch 3-year-old needle mortality, Pcht = proportional height, Avht = mean height during the period, Wc = weeding, CL = clones, CA1 = initial crown photo area, CA2 = final crown photo area, RelCA = relative crown photo area and Avwhl = average whorls during the period.

Residual plots for branch needle mortality are shown in Figures 5.46 to 5.49.

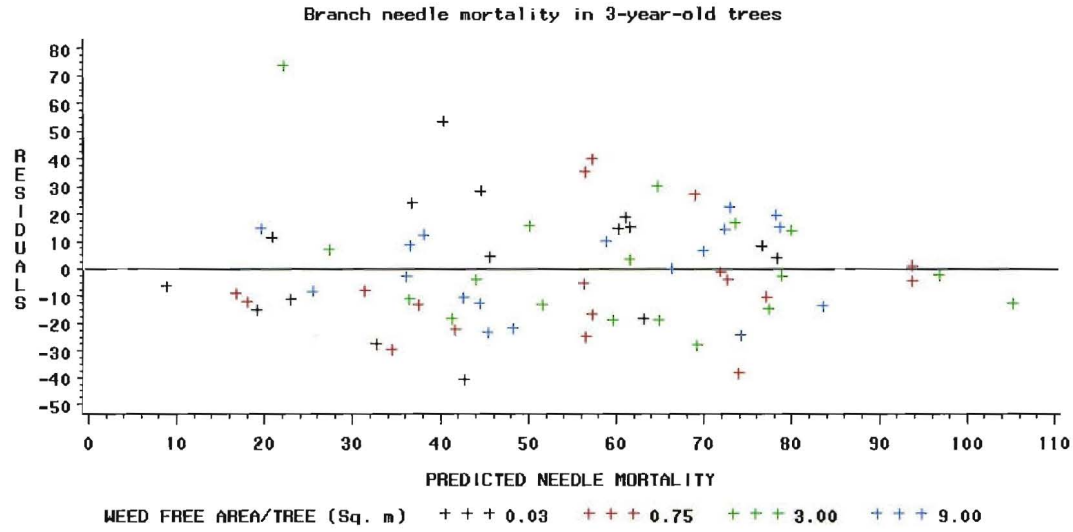

Figure 5.46: Residuals vs. predicted values for branch needle mortality

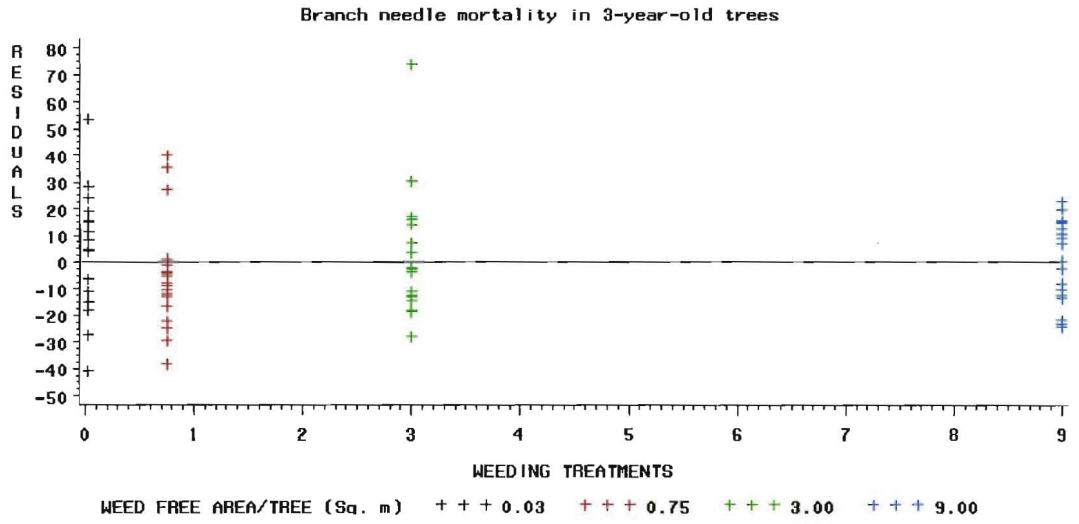

Figure 5.47: Residuals vs. weeding treatments for branch needle mortality

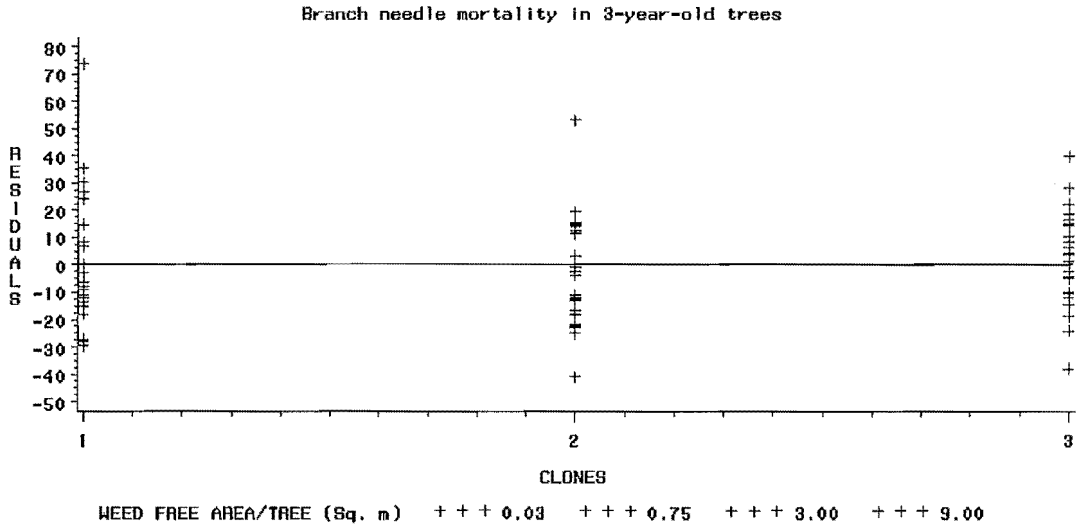

Figure 5.48: Residuals vs. clones for branch needle mortality

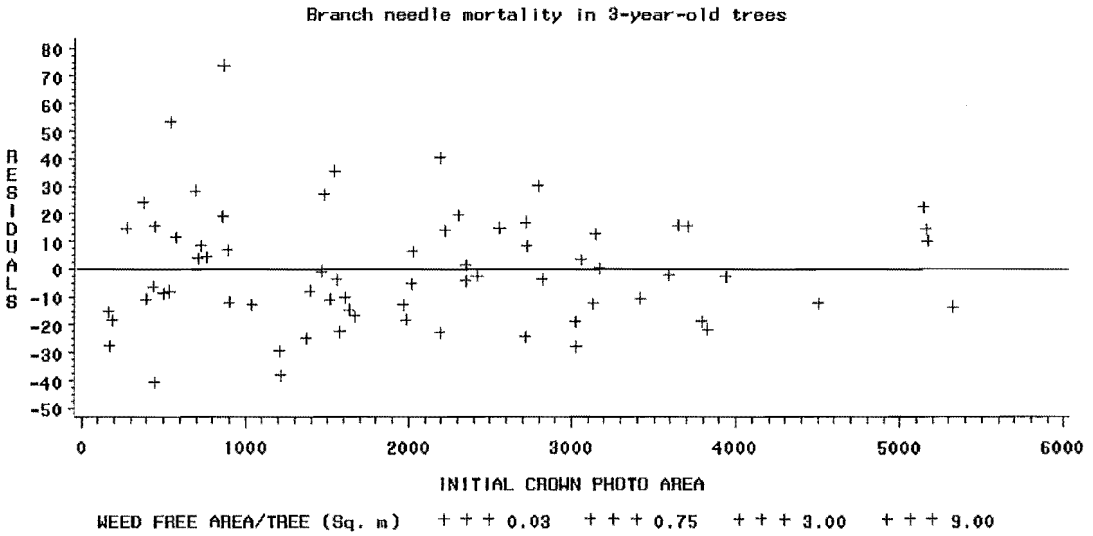

Figure 5.49: Residuals vs. initial crown photo areas for branch needle mortality

Pots of residuals for needle mortality from the stems of 3-year-old radiata pine trees are shown in figures 5.50 to 5.54. The plots showed acceptable trends with little bias.

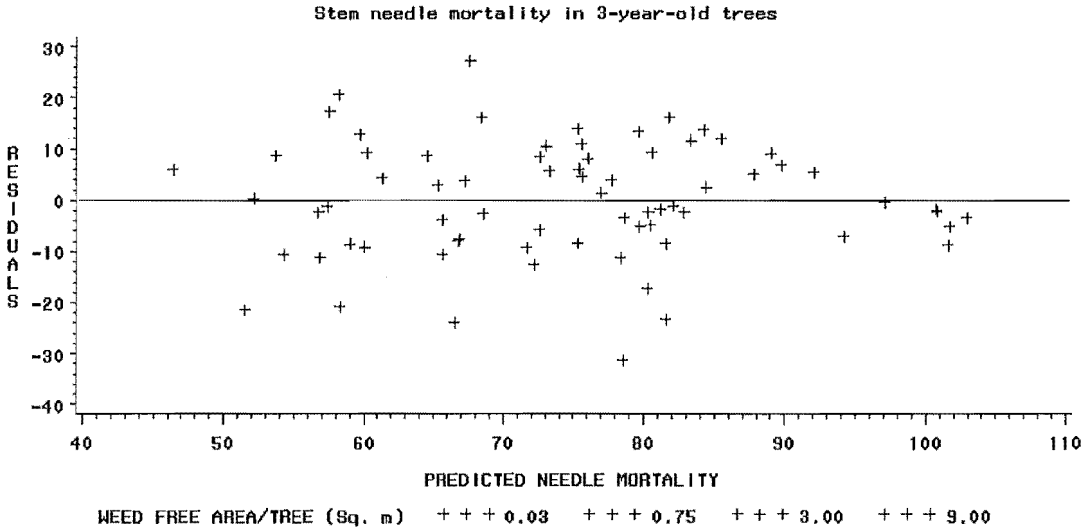

Figure 5.50: Residuals vs. predicted values for stem needle mortality

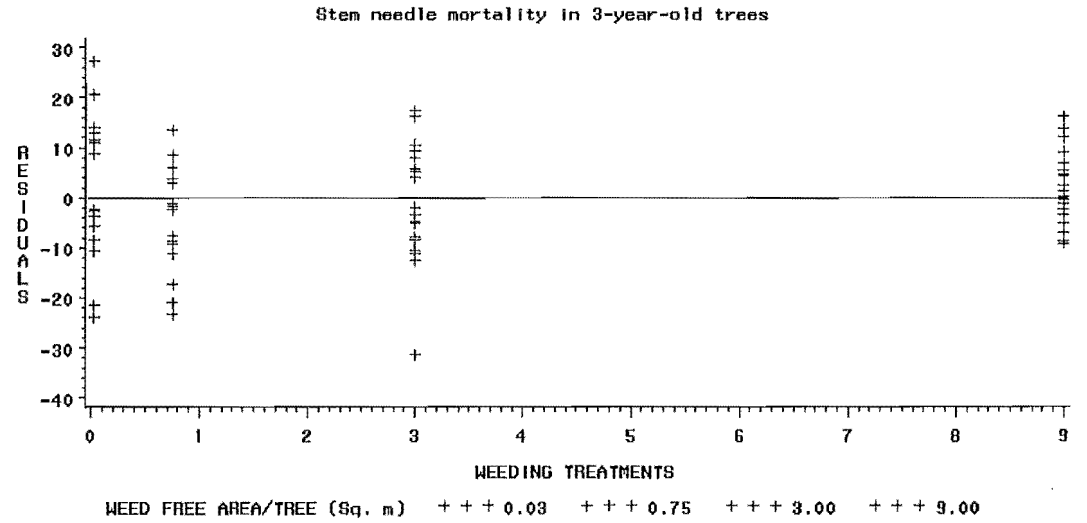

Figure 5.51: Residuals vs. weeding treatments for stem needle mortality

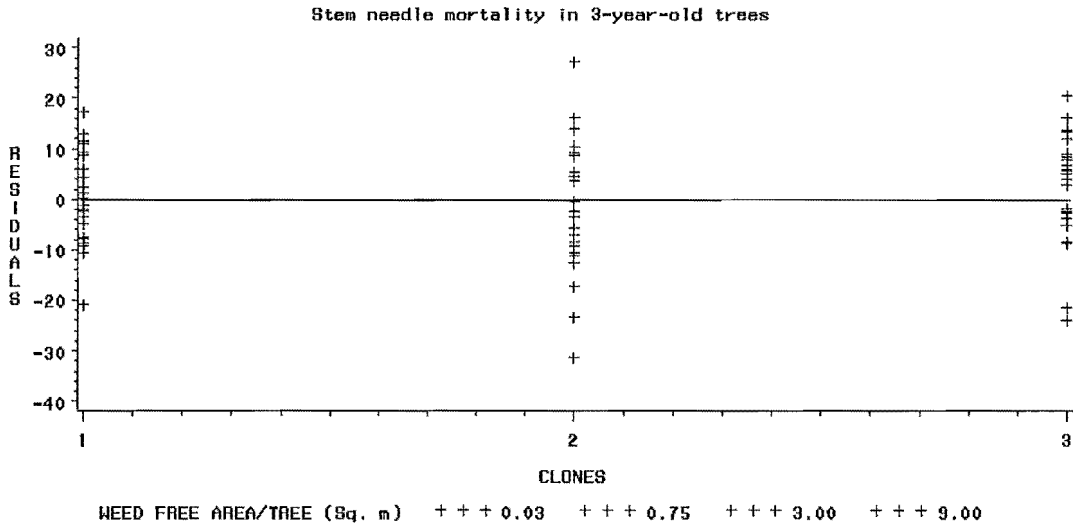

Figure 5.52: Residuals vs. clones for stem needle mortality

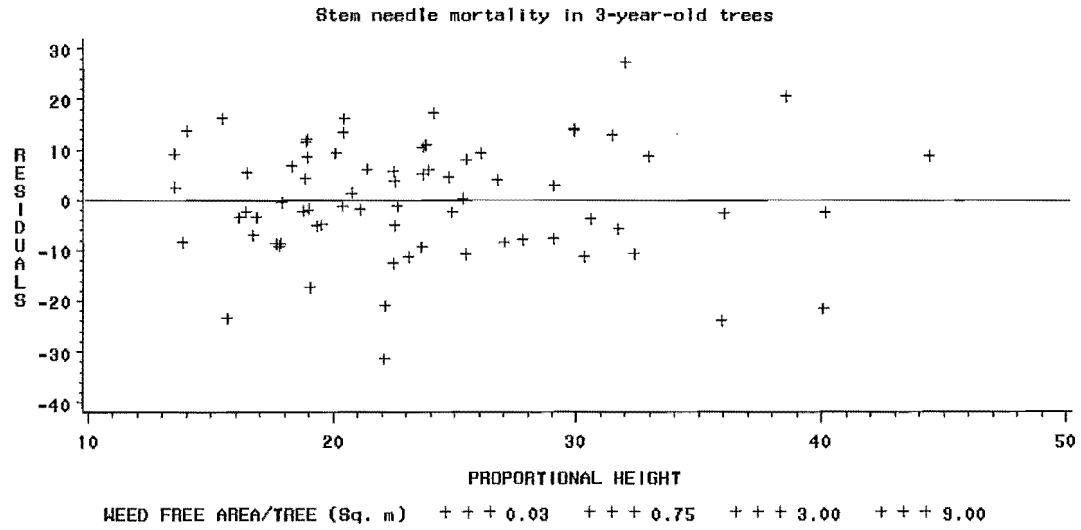

Figure 5.53: Residuals vs. proportional height for stem needle mortality

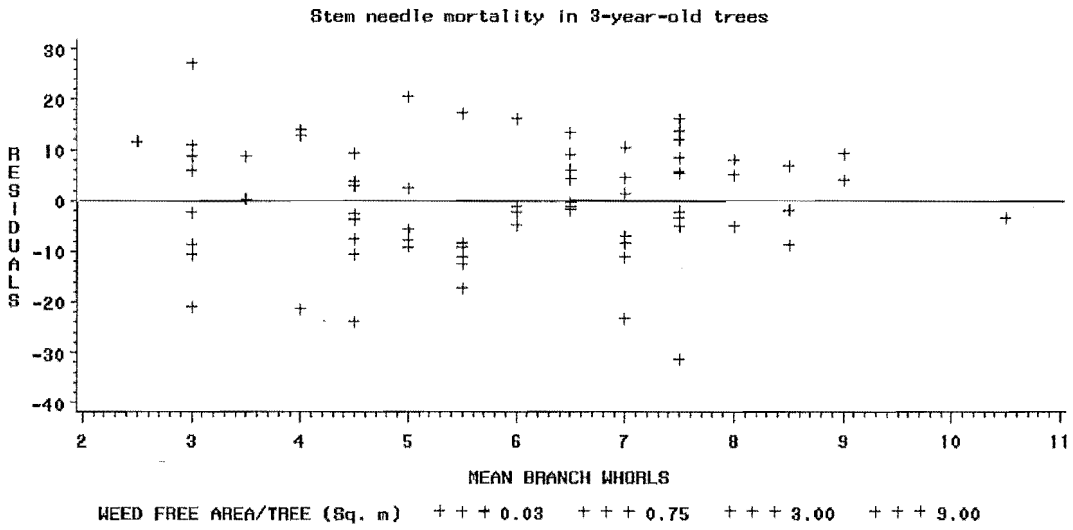

Figure 5.54: Residuals vs. mean branch whorls for stem needle mortality

Trees in weedy plots had proportionally more older foliage present at the end of the study period (period 2) than their counter parts in weeded plots (Figure 5.55). Distance from the treetop was tried but it was not as important as proportional height (statistically insignificant at $\alpha = 0.05$).

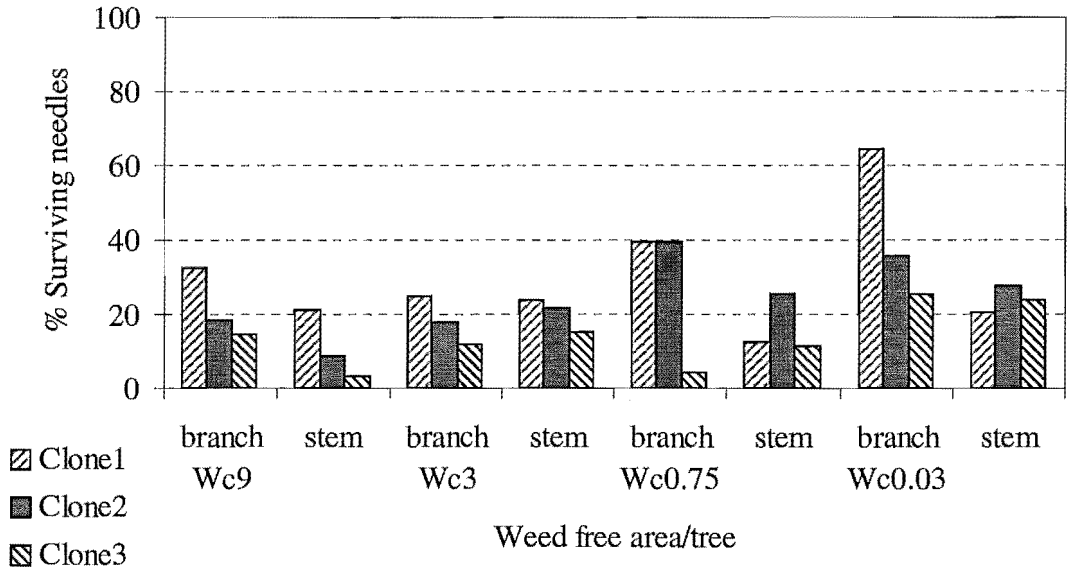

Figure 5.55: Percentage of needles remaining after the second period.

Mean survival values of 3-year old needles were; clone 1 = 29.7 %, clone 2 = 25.3 % and clone 3 = 13.7 %. Mean 3-year old needle survivals for weeding treatments were Wc9 = 16.5 %, Wc3 = 18.9 %, Wc0.75 = 21.4 % and Wc0.03 = 28.4 %.

5.4 DISCUSSION

Needle mortality was successfully expressed in relation to canopy region (stem or branch). Needle age was a significant factor influencing needle death, so were weeding treatments, clones, tree size and crown characteristics (e.g. crown position, number of whorls during the period, proportional height and relative crown photo area). While needle mortality was theoretically envisaged to follow a logistic equation, no meaningful overall model could be developed due to paucity of data especially during the actual period of intensive needle senescence (December to March). This is because data were collected in winter and not during the growing season when apparently most needles were actually dying; an invaluable lesson indeed.

Proportional height was a significant variable influencing needle mortality and not height from the top. Proportional height was calculated as;

$$\frac{\textit{Height above ground showing needle mortality}}{\textit{Total tree height}} \qquad (5.21)$$

Height from the top was thought initially to be a good surrogate for light extinction as canopy depth increased. However, proportional height was a better surrogate for within crown environment, probably including light conditions.

The use of proportional height may be explained in terms of crown size. Trees with large crowns are theoretically expected to be taller and show higher needle mortality. The mortality of needles is influenced by height above ground of the sampling unit as well as the crown size as a whole. Proportional height has a weighting effect for tree size. Raw height from the top poorly represents within tree crown environment because of its failure to account for the significant effect tree size has on crown

processes. Using raw height from the top is tantamount to assuming that any two trees will have similar within crown environments (light, water vapour, temperatures) at points of equal distance from the top irrespective of crown size. This has been shown to be untrue (e.g. Xu 2000). This may point to the fact that models which assume crown environments to be uniform (e.g. EARLY (West *et al.* 1982) which uses crown length) may need more sensitive and realistic measures of within crown environment.

Needle mortality sampling units were systematically allocated to stem and branch sections from the bottom of the crown outwards. There could be concerns that the lack of complete randomisation compromised the validity of the tests and the outputs from the ANOVA procedures, but the use of regression rather than ANOVA allows a valid analysis. Answers were obtained to the following questions:

1) where did most needle mortality occur within the crowns?
2) what were the relative losses from the stem and branches?
3) how did mortality vary with needle age and crown size?
4) how was mortality related to weeding gradients or clones?

These questions could not be succinctly answered by randomly allocating needle sampling units to any position within the crowns, but by systematic and methodical approaches accounting for every stem and branch segment within the crown. In this regard the study was very informative; demonstrating that significant needle mortality occurred in needles which were 3 years or older and from the stem outwards and from the bottom of the crown upwards subject to crown size and the amount of new foliage added.

In summary, valuable insights were gained regarding the processes of fascicle mortality in juvenile trees. These were that in young trees (up to age 3) needle age, genetics, weeding (effects on tree size and needle growth) and crown size were important factors determining needle mortality. The observation that mortality of stem needles was much higher and significantly different to branch needles raises important questions regarding the accuracy of crown models which assume the

average conditions within crowns to be uniform and emphasises the need to test models with better estimates of within crown processes.

Detailed knowledge of needle mortality patterns accounting for both spatial and temporal changes will increase the sensitivity of current leaf area and c-fixation models.

One of the major recommendations from the study is that future investigations should be carried out at least every week especially during the period of fast needle development (December - March). This will make it feasible to fit a meaningful logistic equation to the data. It is, therefore inconclusive from this study whether needle mortality did or did not follow a synchronized pattern with needle development as reported in other studies (e.g. Kinerson *et al.* 1974). Moreover, fascicle mortality appeared to be a direct consequence of light conditions within the canopies. This is due to the fact that most needle deaths occurred in 3-year-old foliage on the stem, where shading was expected to be most intense. As such trees with sparse crowns or those growing in weed infested plots may "hang-on" to most of their older foliage due to their more open crowns. Thus future studies may also need to integrate aspects of light conditions within the canopies.

5.5 CONCLUSIONS

1) Two models of needle mortality were fitted, one using all the data and the other based on 'average' tree characteristics. This was seen as an invaluable step towards a true representation of the dynamic processes of tree crowns and a worthy module in a phenomenological (mixed) model. A tree-based model should include actual light measurements and photosynthesis measurements in addition to crown structure measures. These measurements should be made at the same time(s) and on the same subject trees.

2) Needle mortality from the stem of 3-year old trees was a function of proportional height, crown photo area (an estimate of leaf biomass) and whorl numbers.

$$Mort_{St} = 127.031 - 1.1065 * Pcht + 7.521 * Avwhl + 0.00323 * CA_2 - 0.0311 * \mathrm{Re}lCA - 0.499 * Avht \qquad (5.19)$$

3) Needle mortality from the branches of 3-year old trees was a function of genotype, genotype*weeding interaction and crown photo area (an estimate of foliage biomass).

$$Mort_{Br} = 25.369 + 18.9820 * CL - 1.458 * CL * Wc + 0.00953 * CA_1 + 0.05044 * \mathrm{Re}lCA \qquad (5.20)$$

4) Needle age, genetics, weeding treatment and crown size were important factors determining needle mortality.

5) Mortality of stem needles was much higher and significantly different to that observed on branches.

SYNTHESIS OF CROWN FOLIAGE BUDGETS STUDIES

The study of crown foliage budgets is a diverse field with many interacting factors. In this study some of the important factors thought to influence leaf area additions and losses were quantified. From the inputs generated by the specific studies, overall models of crown foliage budgets were developed and used to estimate the amount of leaf area by age class after accounting for leaf area losses. Some of the variables especially total tree biomass, leaf weight and leaf area were later used in relative growth rate studies (Chapter 6).

It was demonstrated that different clones had different growth and above ground allocation strategies. The differences in leaf area additions led to differences in leaf area losses but these may have been moderated by crown structure with small crowns losing less leaf area.

By estimating leaf area additions and needle mortality and calculating the net gains in leaf area, more realistic and biologically meaningful crown foliage budgets were developed. Some refinements are needed especially with respect to the time frame for counting dead needles and these were duly raised in part II of this chapter. By combining leaf area growth dynamics and allocation patterns with leaf area losses, this study served an important facet in the quest for realistic mechanistic models of crown production and thereby serves as a beacon for future studies.

A major limitation was the lack of any specific studies on below ground allocation patterns. Root growth dynamics can influence above ground biomass allocation patterns considerably, and future studies should include this aspect.

CHAPTER 6

PLANT GROWTH AND RELATIVE GROWTH RATE

6.1 OVERVIEW

Relative growth rate (RGR) is defined as the ratio of the growth of an organism to its size at the beginning of the growth period. While the calculation of mean relative growth rate ($\overline{RGR}$) is simple, the use of RGR and the interpretations attributed to the results have been of considerable interest and the source of major debate among scientists and researchers of plant growth analysis. Of great interest was the assumption that ($\overline{RGR}$) removed size related differences and that ($\overline{RGR}$) was "constant".

In this chapter the RGR expansion is presented and the validity of the assumptions for constant RGR is investigated. Changes in mean relative growth rate as a function of time and tree size were followed through the first 3 years of tree growth by quantifying the morphological and physiological terms of the RGR expansion. Reasons for the decline in RGR with time and size are discussed.

6.2 QUANTIFYING PLANT GROWTH

6.2.1 Background

The foundations of plant growth analysis were laid down by researchers (e.g. Gregory 1926, 1928, Blackman 1919, Briggs *et al.* 1920, West *et al.* 1920, Fisher 1921) in the early part of the 20th century. The approaches used by these researchers

largely involved fitting curves to data to 'smoothen' empirical relationships. The use of sound mathematical approaches became available in the late 1960s following advances in the field of statistical theory and experimentation. The availability of powerful electronic computers further enhanced data analyses procedures and allowed fitting of complex functions (especially non-linear) to growth data.

6.2.2 Definitions: growth, growth rate and relative growth rate

6.2.2.1 Growth

Growth can be defined as the permanent increase in the number of cells and/or size of an organism as a result of physiological and morphological changes within the organism (Causton and Venus 1981, Hunt 1982).

$$Growth = W_2 - W_1 \qquad (6.1)$$

where;

W_1 and W_2 are size at time 1 and 2 respectively.

6.2.2.2 Growth rate

Growth rate is defined as the magnitude of change in number or size of an organism with time. Mathematically, this can be expressed as:

$$Growth\ rate = \frac{Change\ in\ size, (dW)}{change\ in\ time, (dT)} \qquad (6.2)$$

In plants, the main assumption is that increase in dry weight depends solely on photosynthesis although plants in the dark or under very low light may have negative or low growth as photosynthesis rates are below respiration levels.

6.2.2.3 Relative growth rate (RGR)

Briggs *et al.* (1920) first used the term relative growth rate, although Blackman (1919) had used it previously under the name "efficiency index". Relative growth rate (RGR) is defined as the average rate of growth per unit weight. Mathematically it can be expressed as:

$$RGR = \frac{dW}{dT} * \frac{1}{W} \qquad (6.3)$$

RGR was used extensively with data from annual crops in agriculture. Its use in perennial plants (e.g. trees in forestry) may result in discrepancies considering that perennial plants remain in the field longer. Thus prolonged exposure to the environment may affect the allometric relationships of various plant parts differently. Moreover, considering that plant growth is a function of many factors (e.g. temperatures, photoperiod, moisture, light quantity and quality, nutrients and genetics) acting on the initial tree size, RGR may change considerably depending on the size (leaf area) and the prevailing environmental conditions.

Mean relative growth rate, $\overline{RGR} = \frac{\ln(W_2) - \ln(W_1)}{T_2 - T_1}$ (6.4) (Hunt 1982, Evans 1972)

has been used extensively as a measure of plant "efficiency" in producing new dry matter (Van den Driessche and Van den Driessche 1991, Evans 1972, Hunt 1982, Causton 1983, Brand 1991, Harrington and Tappeiner II 1991, Ledig and Perry 1969). It has been reported to remove "size related" differences (e.g. Sweet and Wareing 1966, Wareing 1966, Causton and Venus 1981, Brand 1991, Hunt 1982, van den Driessche 1992,). Several researchers have questioned this assumption however, with examples of studies where $\overline{RGR}$ did not appear to remove size differences (e.g. Burdon and Sweet 1976, Britt *et al.* 1991, Brand *et al.* 1987, South 1991, South 1995, Mason *et al.* 1996a). South (1991) and Mason *et al.* (1996a) concluded that the use of RGR to remove "size related differences" was misleading and had no biological basis. In an attempt to remove the confounding of size, Britt *et al.* (1991) suggested that RGR be compared on an initial size basis rather than at equivalent ages. Mason *et al.* (1996a) derived flexible functions which allowed RGR to vary with time and/or size in a malleable manner.

Relative growth rate has been reported to decrease with plant size due to changes in allometry and especially the increase in non-photosynthetic structural material (i.e. increased allocation to stem vascular tissues (Beets and Pollock 1987, Madgwick 1994)), self-shading of foliage (Britt *et al.* 1991) and physiological aging (Menzies *et al.* 1991). Changes in RGR may also be due to morphological changes especially variation in leaf area ratio (LA/W), or physiological changes in particular variation in unit leaf rate {(dW/dt)*(1/LA)}. Leaf area ratio is very sensitive to factors within the

tree that influence the rate of dry matter production as well as the external environment.

6.2.3 Relative growth rate: is growth directly proportional to size?

6.2.3.1 Case 1: constant RGR

The main assumption behind RGR being constant was that growth is directly proportional to size (Blackman 1919), i.e. $\frac{dW}{dT} = k * W$ (6.5) resulting in a constant relative growth rate; $\frac{dW}{dT} * \frac{1}{W} = k$ (6.6). This presupposes an exponential size-age relationship; $W = \exp(k * T)$ (6.7); where W = plant dry weight, T = time and k = RGR. However, as Mason *et al.* (1996a) argued, this equation is not flexible enough and rarely describes actual growth data (South 1991).

6.2.3.2 Case 2: exponential size-age relationship

If the size-age relationship is of the form $W = \alpha * T^{\beta}$ (6.8), then growth will be

$$\frac{dW}{dT} = \alpha * \beta * T^{\beta-1} \quad (6.9),$$

$$\frac{dW}{dT} = \frac{\beta * W}{T} \quad (6.10) \text{ and}$$

$$RGR = \frac{\beta}{T} \quad (6.11).$$

In this case, RGR is governed by the 'rate and shape' coefficient and time rather than size *per se*. This implies that factors which influence the 'rate and shape' coefficient of the 'size-age' relationship (e.g. weeding, fertilization and genotype) will have profound effects on RGR.

6.2.3.3 Case3: Exponential size-age relationship

This function is similar to case 1 but with a 'β' term as a power making the function more flexible.

$$W = \exp(\alpha * T^{\beta}) \quad (6.12)$$

$$\ln(W) = \alpha * T^{\beta} \qquad (6.13)$$

$$\frac{dW}{dt} * \frac{1}{W} = \alpha * \beta * T^{\beta-1} \qquad (6.14)$$

$$RGR = \ln(W) * \frac{\beta}{T} \qquad (6.15)$$

In this case, RGR is influenced not only by the 'rate and shape' parameter but also by the initial size (its natural logarithm) and time.

South (1991) reports that in practice even in circumstances where the size-age relationship is exponential, the initial size must be set to zero to have a constant RGR. It is important to note that a change in time normally connotes a change in size but there is no direct proportionality. Thus under water stress, for example, changes in time may be poorly correlated to changes in size. South (1991) gave several examples where mean RGR did not follow the "constant" trend even when seedlings followed the same basic growth curve provided they differed in initial sizes. This implied that the morphological and physiological states of the seedlings influenced RGR strongly through their effects on dry matter out-turn, an observation supported by Menzies *et al.* (1991) and Beets and Pollock (1987) who reported physiological age to be more important for tree growth than chronological age. Mason *et al.* (1996a) fitted RGR curves to biomass data loaned from Britt *et al.* (1991) and juvenile tree growth data from the Central North Island, New Zealand loaned from Mason (1992). They derived mathematical equations for RGR by assuming that relative growth rate varied with size and time.

In summary, modellers need to know the explicit size-age relationship of the crop(s) they are dealing with in order to derive accurate RGR functions. Assumptions based on generalized expressions of tree growth should be treated cautiously because several size-age functions that differ in the parameters can end up with the same general dW/dt expression but with quite different RGR (South 1991). Thus while there are instances when growth can be directly proportional to size (i.e. a special case of exponential growth, $W = \exp(k * T)$ (6.16)) this may not always be so and is better treated as an exception rather than the rule.

6.3 COMPONENTS OF RELATIVE GROWTH RATE

RGR has been partitioned into physiological and morphological components to help explain tree structure and functioning (Evans 1972, Causton and Venus 1981). By following the changes in the RGR components brought about by management and/or silvicultural treatments, useful insights can be learnt regarding tree responses to modifications in their growing environments (Radosevich and Oysteryoung 1987, Britt *et al.* 1991).

Evans (1972) expressed RGR expansion as;

$$RGR = \underbrace{\frac{dW}{dT} * \frac{1}{LA}}_{ULR} \times \underbrace{\frac{LA}{Lw}}_{SLA} \times \underbrace{\frac{Lw}{W}}_{LWR} \qquad (6.17)$$

where;

RGR = Relative Growth Rate,

ULR = Unit Leaf Rate ($g/cm^2/day$),

SLA = Specific Leaf Area (cm^2/g) and

LWR = Leaf Weight Ratio.

The following subsections will discuss these components briefly.

6.3.1 Unit leaf rate (ULR)

The unit leaf rate is defined as the rate of dry matter increase per unit leaf area (Briggs *et al.* 1920). It has been called the 'net assimilation rate" by some researchers (e.g. Gregory 1926). It is a measure of foliage efficiency in producing dry matter. Mathematically, unit leaf rate is expressed as:

$$ULR = \frac{dW}{dT} * \frac{1}{LA} \qquad (6.18)$$

where;

dW/dT = instantaneous rate of dry matter change and

1/LA = reciprocal of the total photosynthesising area of the tree.

The Mean Unit leaf rate ($\overline{E}$) is mathematically expressed as:

$$\overline{E} = \frac{W_2 - W_1}{T_2 - T_1} * \frac{\log(LA_2) - \log(LA_1)}{LA_2 - LA_1} \qquad (6.19)$$

(Evans 1972, Causton and Venus 1981)

In plentiful water and nutrient supplies, the amount and quality of radiant energy reaching the leaves will determine carbon fixation rates; all other factors (e.g. enzymes involved in carboxylation, stomatal numbers, mesophyll resistance and CO_2 concentration) being within normal range for optimal activity. Carbon fixation can be described by the equation;

$$n(CO_2) + n(H_2O) \xrightarrow{light} (CH_2O)n + n(O_2) \qquad (6.20)$$

where;

CO_2 = carbon dioxide,

H_2O = water,

CH_2O = carbohydrates,

O_2 = oxygen and

n = constant for the number of molecules.

It can be seen that the rate of dry weight change and hence net photosynthesis are the main determining factors influencing ULR. Therefore, any condition which reduces net photosynthesis for a given leaf area will affect ULR. For example shading (self or from neighbours as in competition for light), leaf position and angle (will reduce the quantity and quality of light reaching the leaves) and leaf age (will reduce the efficiency with which the leaves can utilize intercepted radiation).

6.3.2 Specific leaf area (SLA)

Specific leaf area is defined as the ratio of leaf area to leaf weight;

$SLA = \frac{LA}{Lw}$ (6.21) (Evans 1972, Causton and Venus 1981, Hunt 1982).

Specific leaf area of a tree shows the average leaf expansion in area per unit leaf dry weight. It shows how the dry weight set to foliage has been invested in 'energy' capturing surfaces (leaf area). It is an anatomical index related to the expansion of the plant's leaf material and therefore, influences leaf structure and development.

The average SLA of a plant may change due to; 1) losses of new or old foliage through death or senescence, browsing or defoliation; 2) growth of new foliage to maturity and 3) expansion of cell wall thickness due to maturation.

6.3.3 Leaf weight ratio (LWR)

LWR is the ratio of total plant foliage weight to plant dry weight;

$$LWR = \frac{Lw}{W} \qquad (6.22)$$ (Evans 1972, Causton and Venus 1981, Hunt 1982).

It shows the proportion of plant dry weight set to foliage. In young trees, which are growing exponentially (before canopy closure), the ratio may change considerably due to increased foliage production (Chapter 5, section 5.3.3 in this thesis).

Leaf weight ratio and specific leaf area together make up leaf area ratio;

$$LAR = \frac{LA}{\underbrace{Lw}_{SLA}} * \frac{\underbrace{Lw}_{W}}{\underbrace{W}_{LWR}} = \frac{LA}{W} \qquad (6.23).$$

LAR is the ratio of the total tree leaf area to tree dry weight and is indicative of the total dry weight invested in photosynthesizing surfaces (foliage). It can be seen therefore that RGR is the product of unit leaf rate and leaf area ratio. By breaking down RGR into ULR and LAR it is possible to relate carbon assimilation to leaf area. Mean Leaf area ratio is mathematically represented as;

$$\overline{LAR} = \frac{LA_2 / W_2 + LA_1 / W_1}{2} \qquad (6.24)$$

where;

$\overline{LAR}$ = mean leaf area ratio,

LA_1 = initial leaf area of the tree,

LA_2 = final leaf area of the tree, and

W_1, W_2 = tree dry weight at the start and end of the study period respectively.

In summary, assuming that the allometric relationships between various plant parts remain constant i.e. fixed ratio of photosynthetic organs to non-productive material, (an unlikely event in real life, and if it occurs then not for long periods of time) RGR will be higher in plants with high proportions of leaf area. More specifically, trees with higher dry weight turn-over per unit leaf area (unit leaf rate) and those with higher ratio of leaf area to total dry weight (LAR) will have higher RGR.

The objectives of this chapter are three-fold:

1) to show the effects of varying weed comptition on mean RGR;
2) to show how the mean RGR of three clones 1, 2 and 3 varies with tree age and size; and
3) to show which of the two assumptions for constant RGR, i.e. (i) constant assimilation rate per unit leaf area (ULR) and (ii) constant ratio of total plant leaf area to dry weight (LAR) were broken.

6.4 METHODS

Mean RGR was calculated using three approaches: 1) total above ground biomass, equation 6.25; 2) the expansion terms, equation 6.17; and 3) the expansion terms but weighting for leaf efficiencies of the various leaf-age categories. Mean relative growth rate was calculated for each tree in the experiment using the equation; $\overline{RGR} = \frac{\ln(W_2) - \ln(W_1)}{T_2 - T_1}$ (6.25). The terms of the RGR expansion (RGR = ULR*SLA*LWR; equation 6.17) were quantified using the values of total tree biomass (W), leaf weight (Lw) and leaf area (LA) calculated at tree ages 1, 2 and 3 as described earlier in chapter 5 part I. The specific equations used were;

$$\overline{E} = \frac{W_2 - W_1}{T_2 - T_1} * \frac{\log(LA_2) - \log(LA_1)}{LA_2 - LA_1}$$ (equation 6.19)

to calculate mean unit leaf rate and

$$\overline{LAR} = \frac{LA_2/W_2 + LA_1/W_1}{2} \quad \text{(equation 6.24)}$$

to calculate mean leaf area ratio.

Relationships between crown photo area versus leaf dry weight and crown photo area versus total tree dry weight were used to estimate standing tree foliage biomass and total above-ground biomass respectively. Theoretically, functions developed from stem dry weight vs. GLD^2*H and branch dry weight vs. GLD^2*H should have been used to estimate total tree biomass. However, these were not used due to the concerns raised in chapter 5 (part I, section 5.4). The following equations were used:

1) total tree biomass,

   $Total\ tree\ drywt = \alpha * (Crown\ \mathrm{Im}age\ area)^{\beta}$ (equation 5.14);

2) total tree leaf weight (Lw) - from leaf weight versus crown photo area relationship,

   $Leaf\ drywt = \alpha * (Crown\ \mathrm{Im}age\ area)^{\beta}$ (equation 5.13); and

3) total tree leaf area (LA) - from leaf area versus leaf weight relationship

   $Foliage\ Area = \alpha + \beta * Leaf\ dry\ weight$ (equation 5.12).

Estimates of needle mortality (see chapter 5 part II) were used to adjust for losses in leaf area at ages 2 and 3. The predicted leaf area was partitioned into age classes as follows: $PredLA_{T1}$, $PredLA_{T2}$ and $PredLA_{T3}$ = the total predicted leaf area present on the tree at tree ages 1, 2 and 3 respectively. $NewLA_{T1}$, $NewLA_{T2}$ and $NewLA_{T3}$ = one-year-old fully expanded foliage at tree ages 1, 2 and 3 respectively and $NetLA_{T2}$ and $NetLA_{T3}$ = surviving 2-year- and 3-year-old foliage present at tree ages 2 and 3 respectively.

The following expressions were used.

1) New foliage present at tree age 1: $NewLA_{T1} = \mathrm{Pr}edLA_{T1}$ (6.26)

2) At tree age 2 there were some significant needle losses in trees in Wc0.03.

   $NewLA_{T2} = \mathrm{Pr}edLA_{T2} - NetLA_{T1}$ (6.27)

3) At tree age 3 there were massive deaths of 3-year-old needles.

$$NewLA_{T3} = \Pr edLA_{T3} - (NewLA_{T2} + NetLA_{T1}) \quad (6.28)$$

Carbon fixation potential was calculated by weighting each leaf age class by its light use efficiency[1] as reported by Xu (2000). Thus age 1 foliage was given a weight of 1, age 2 foliage a weighting of 0.70 and age 3 foliage a weighting of 0.40. The weighted values were calculated as follows.

1) At tree age 1 the carbon fixation potential was given by,

$$Cfix_{T1} = NewLA_{T1} \times 1 \quad (6.29)$$

2) At tree age 2 the carbon fixation potential was calculated as,

$$Cfix_{T2} = (NewLA_{T2} \times 1) + (NetLA_{T1} \times 0.70) \quad (6.30)$$

3) At tree age 3 the carbon fixation potential was,

$$Cfix_{T3} = ((NewLA_{T3} \times 1) + (NewLA_{T2} \times 0.70) + (NetLA_{T1} \times 0.40)) \quad (6.31)$$

In all cases C-fix$_{Ti}$ = carbon fixation potential of the tree in the ith year after weighting the leaf area of the various leaf age classes by their PAR use efficiency.

The following equations were fitted to the mean RGR data.

1) An equation for constant relative growth rate, $RGR = k$ (6.32)

2) An equation allowing for changes in mean RGR due to tree size and age, $RGR = \ln(W) * \frac{\beta}{T}$ (6.15) derived from $W = \exp(\alpha * T^{\beta})$ (6.12).

3) An exponential decay function $RGR = a + b * \exp(-c * W)$ (6.33).

In all cases RGR = relative growth rate, W = tree biomass, a, b and c are coefficients and k = constant.

[1] Light use efficiency here is used to imply the proportion of final products of photosynthesis a leaf will produce given the same light conditions.

6.5 RESULTS

6.5.1 Relative growth rate (RGR)

Individual tree mean relative growth rate ($\overline{RGR}$) decreased with time and tree size for trees growing in Wc9, Wc3 and Wc0.75 (Figure 6.1). However, $\overline{RGR}$ increased with both time and size for trees in the control, Wc0.03 (Figure 6.4). These trends were consistent whether the initial size was total tree biomass or foliage weight. $\overline{RGR}$ rose steadily with increasing weed free area per tree with trees in Wc0.03 showing the lowest values (Figure 6.2). Clone 3 had lower $\overline{RGR}$ than the other 2 clones (Figure 6.3).

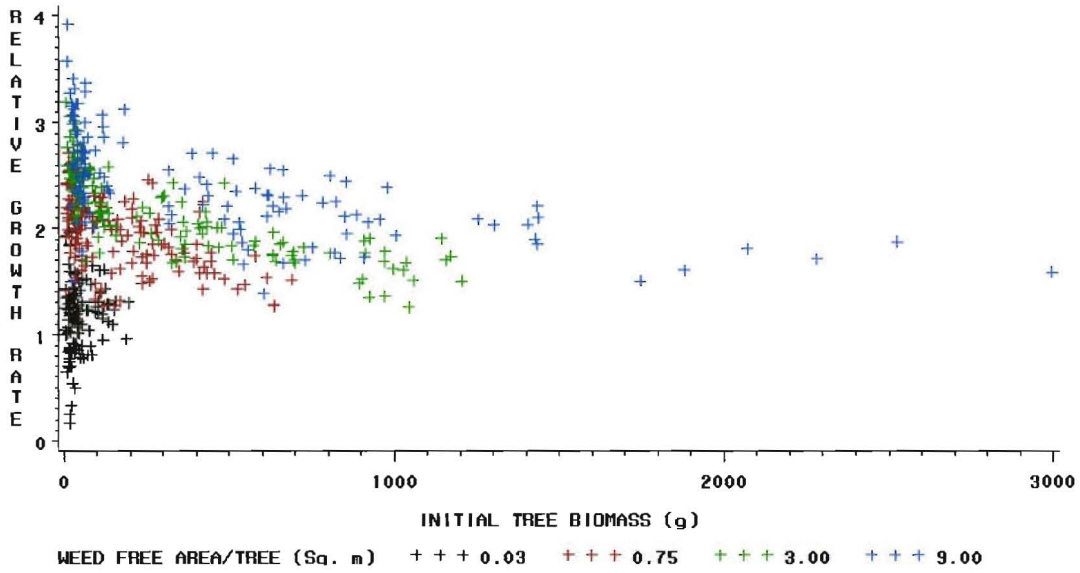

Figure 6.1: Mean relative growth rate ($\overline{RGR}$) versus initial tree above ground biomass. The legend shows Wc9 = blue, Wc3 = green, Wc0.75 = red and Wc0.03 = black colour.

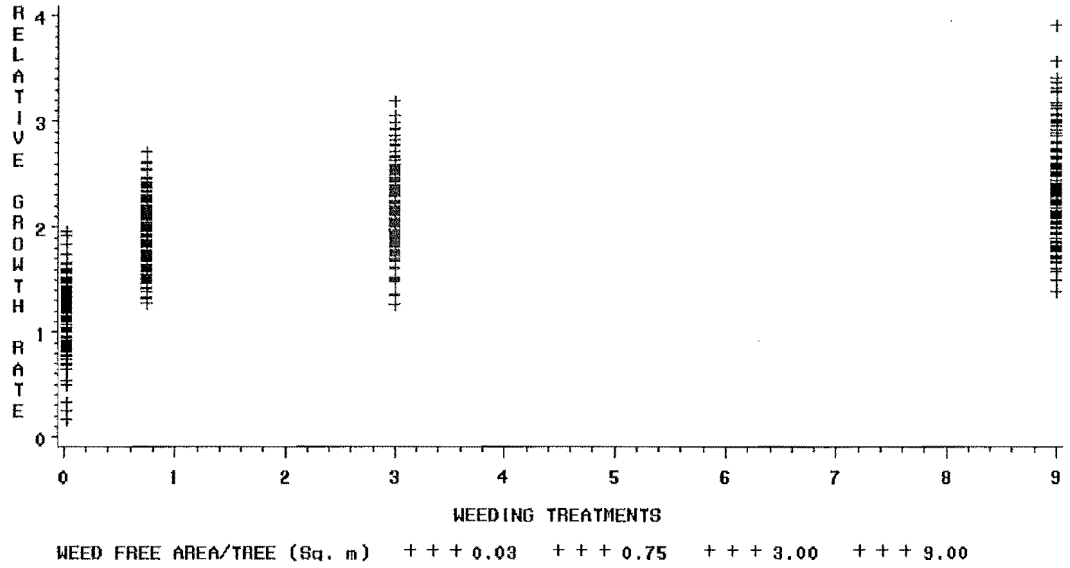

Figure 6.2: Mean relative growth rate ($\overline{RGR}$) versus increasing weed free area per tree.

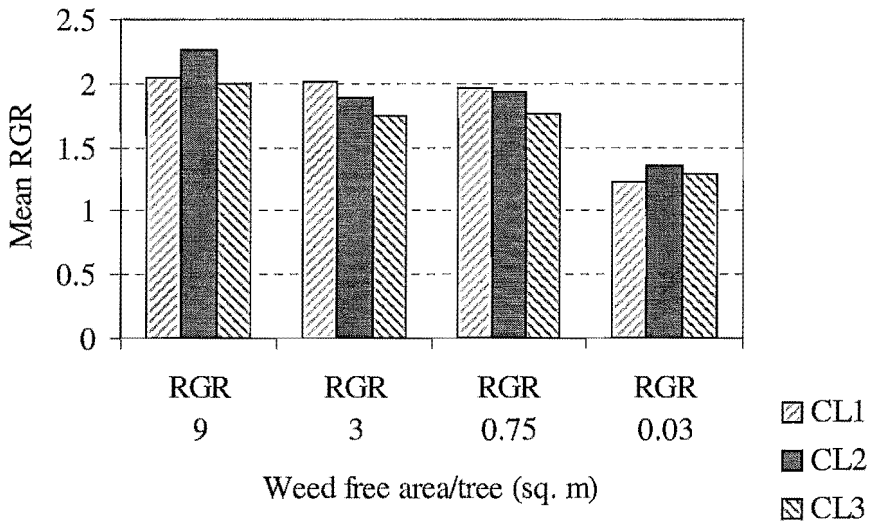

Figure 6.3: Mean relative growth rate of clones 1, 2 and 3 versus weed free area per tree (sq. m) at age 3.

Weighting the leaf area by its PAR use efficiency of the various foliage age classes did not change the declining trend in $\overline{RGR}$ with time and size for trees in the weeded treatments nor the increasing trends for trees in the control. However, it resulted in slight increases in $\overline{RGR}$ values for clones 1 and 2, and reduced $\overline{RGR}$ values for clone 3 (Figure 6.4).

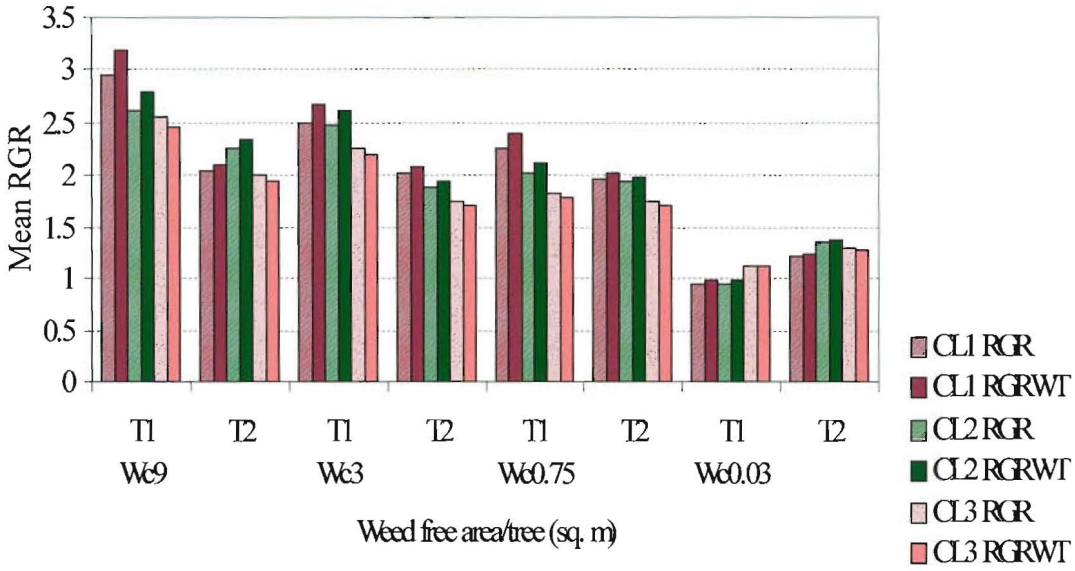

Figure 6.4: Weighted (blocked) and un-weighted (striped) mean relative growth rate for clones 1, 2 and 3 versus weed free area per tree at times 1 (T1) and 2 (T2).

6.5.1.1 Result of fitting the constant relative growth rate (RGR = k) model

The RGR = k model (i.e. constant relative growth rate with size and time) was biased with age and especially tree size (Figure 6.6). It was evident from figure 6.6 that change in tree size was the major cause of the bias. Plots of residuals are shown in figures 6.5-6.8.

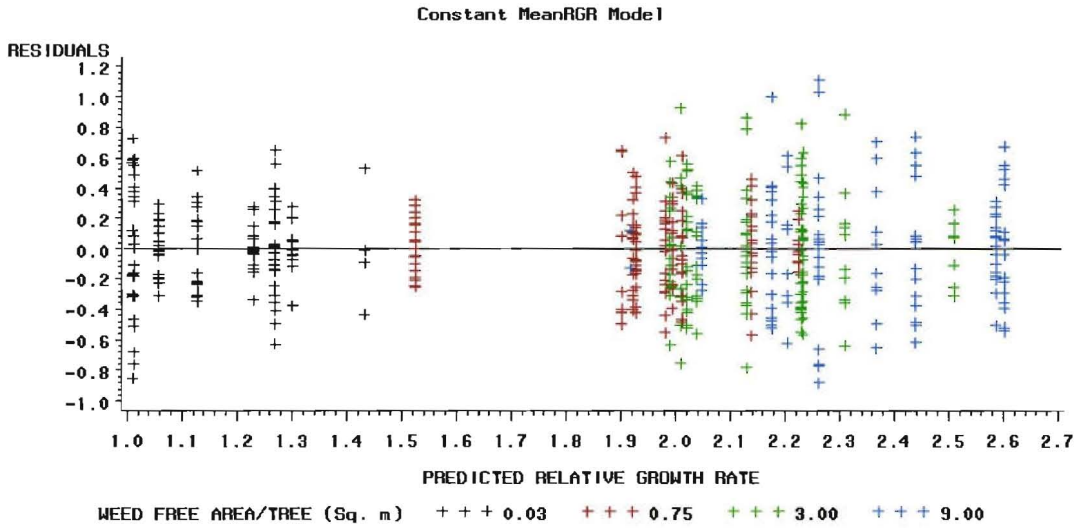

Figure 6.5: Plot of residuals by predicted for the RGR = k model.

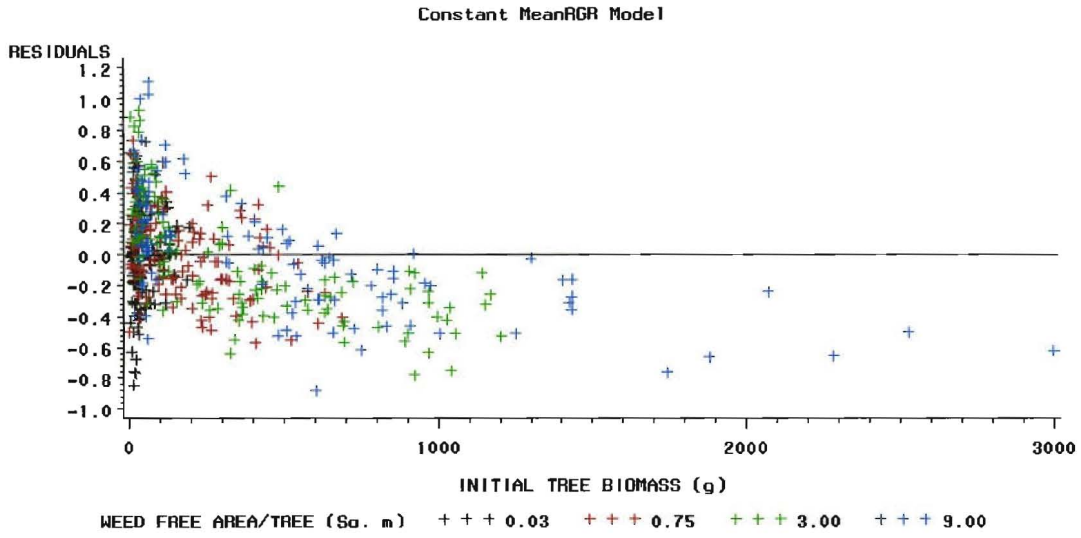

Figure 6.6: Plot of residuals by initial tree size (biomass) for the RGR = k model.

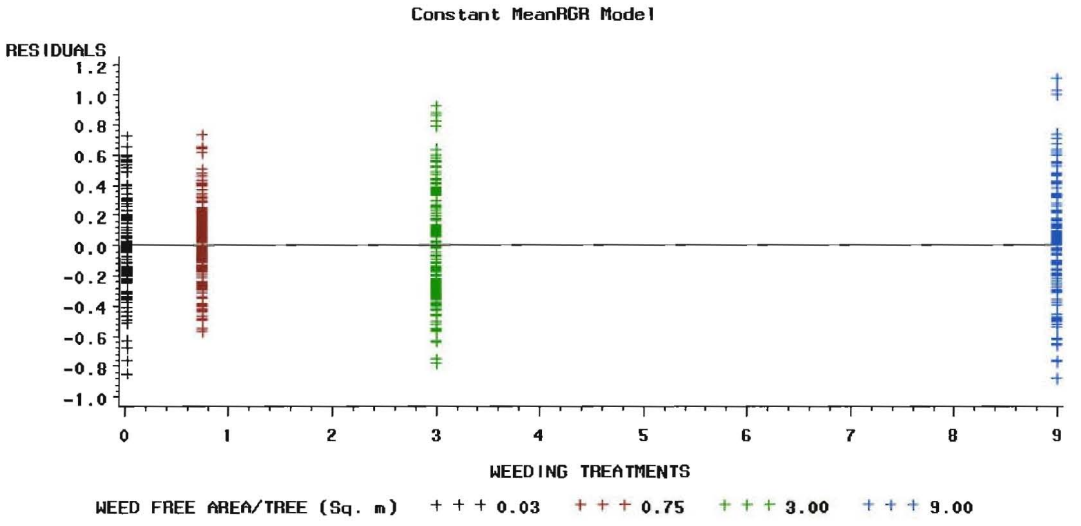

Figure 6.7: Plot of residuals by weeding treatments for the RGR = k model.

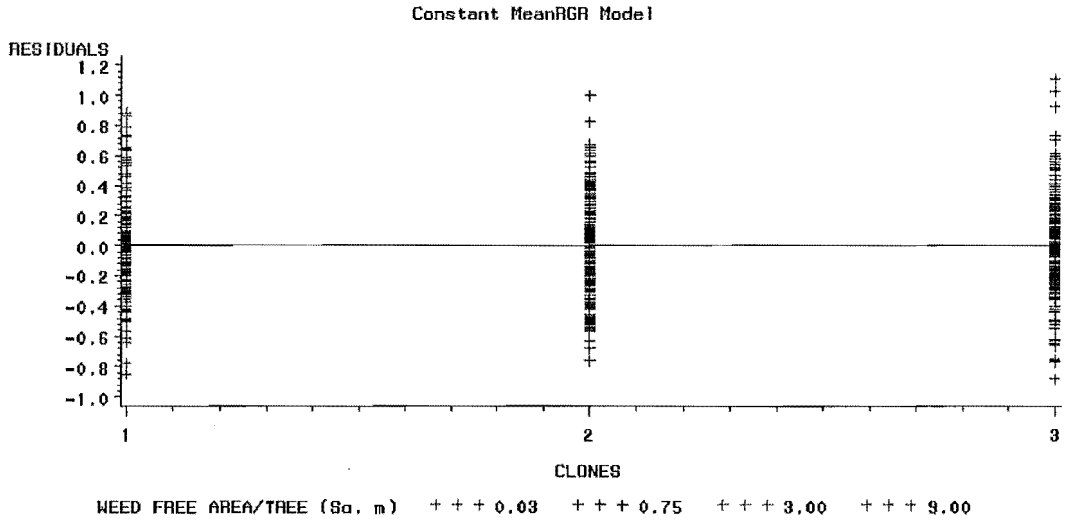

Figure 6.8: Plot of residuals by clones for the RGR = k model.

6.5.1.2 Allowing RGR to vary with size and age

An exponential decay model with dummy variables for weeding treatments and clones best described $\overline{RGR}$ changes with initial tree size (biomass). The function was;

$$\overline{RGR} = a + b * \exp(-c * totbio2) \qquad (6.33)$$

where;

$a = a_0+a_1*Wc0.75$, $b = b_0+b_1*Wc0.03$ and $c = c_0+c_1*Wc3$.

Using initial foliage biomass rather than initial tree biomass in the model achieved similar results (data not shown). Plots of residuals versus predicted values, weeding treatments and clones did not show any apparent bias (Figures 6.9 - 6.14). The residual plots were similar for $\overline{RGR}$ expansion and weighted $\overline{RGR}$. The model outputs are summarized in table 6.1.

Table 6.1: Outputs of the exponential decay model fitted to the mean RGR data.

Coefficients	Biomass RGR	Expansion RGR	Weighted RGR
Residual MSE	0.08548	0.100698	0.099558
Mean	0.000072	-0.00000132	0.000084
Skewness	-0.23551	-0.12496	-0.13953
Kurtosis	0.6513	0.6632	0.7054
a0	1.73979	1.7624	1.77224
a1	-0.57142	-0.62056	-0.6262
b0	0.940118	1.03586	1.04778
b1	-1.55955	-1.67324	-1.69437
c0	0.001316	0.001502	0.001557
c1	0.003669	0.004436	0.004578

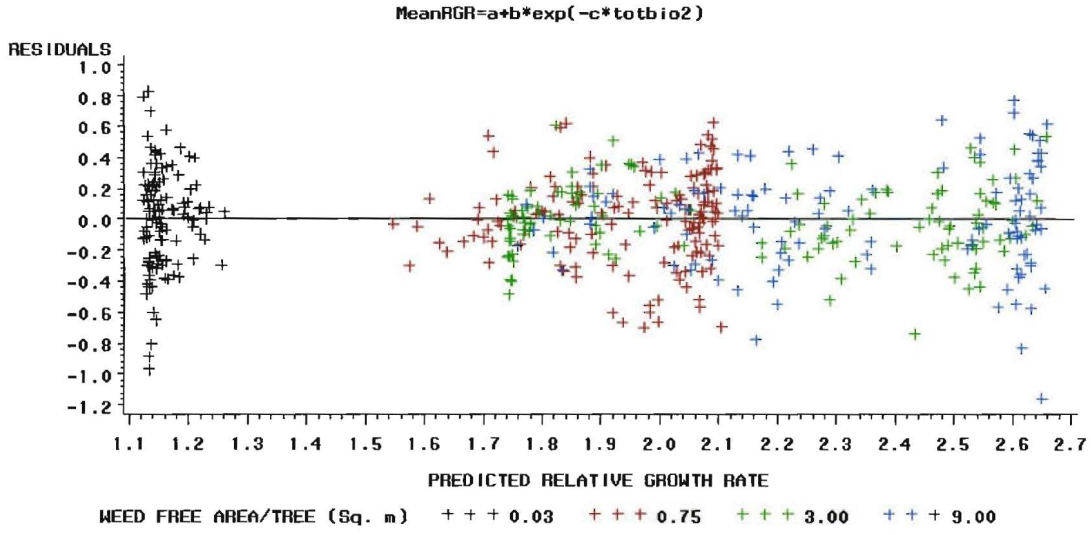

Figure 6.9: Plot of residuals versus predicted mean RGR.

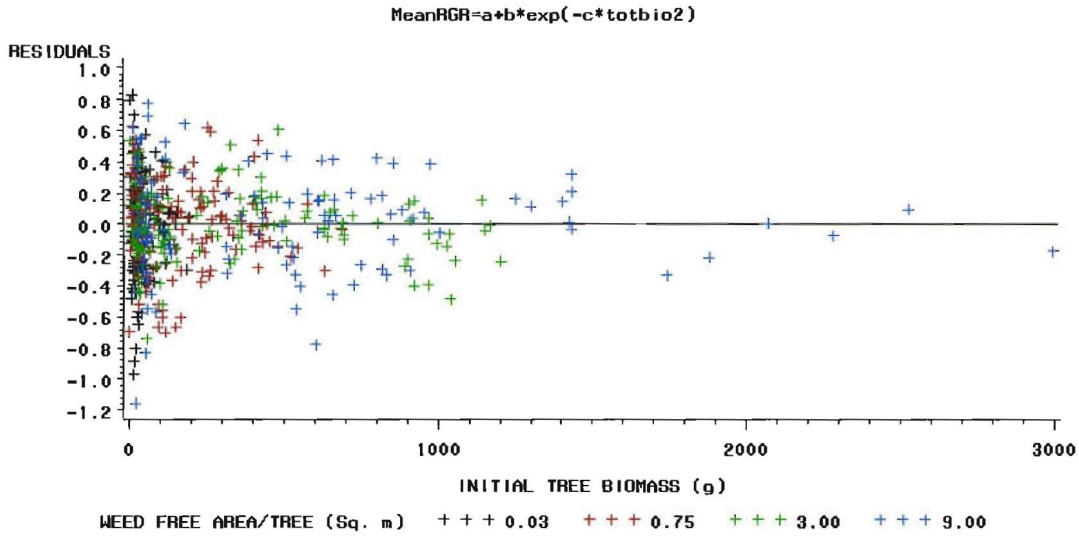

Figure 6.10: Plot of residuals versus initial tree biomass.

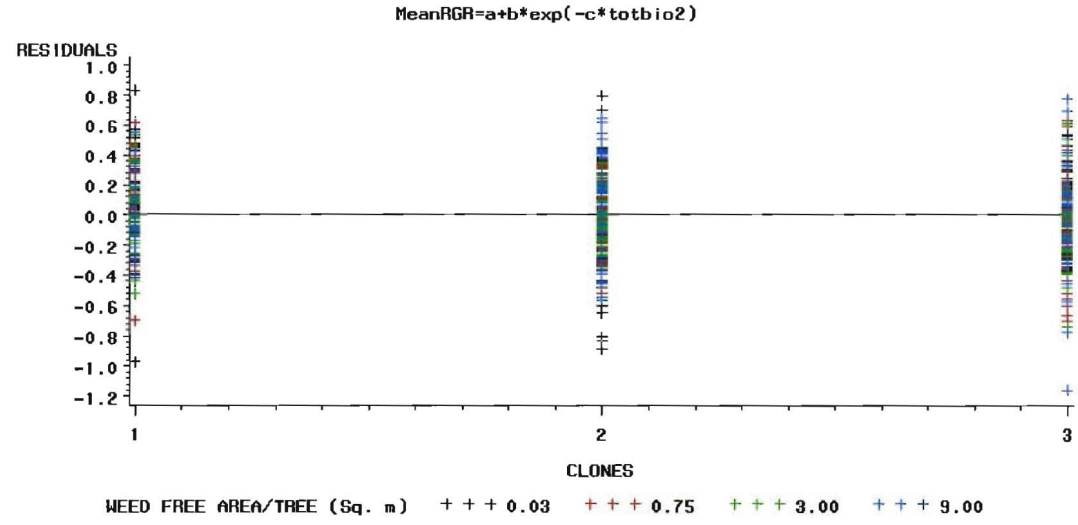

Figure 6.11: Plot of residuals versus clones.

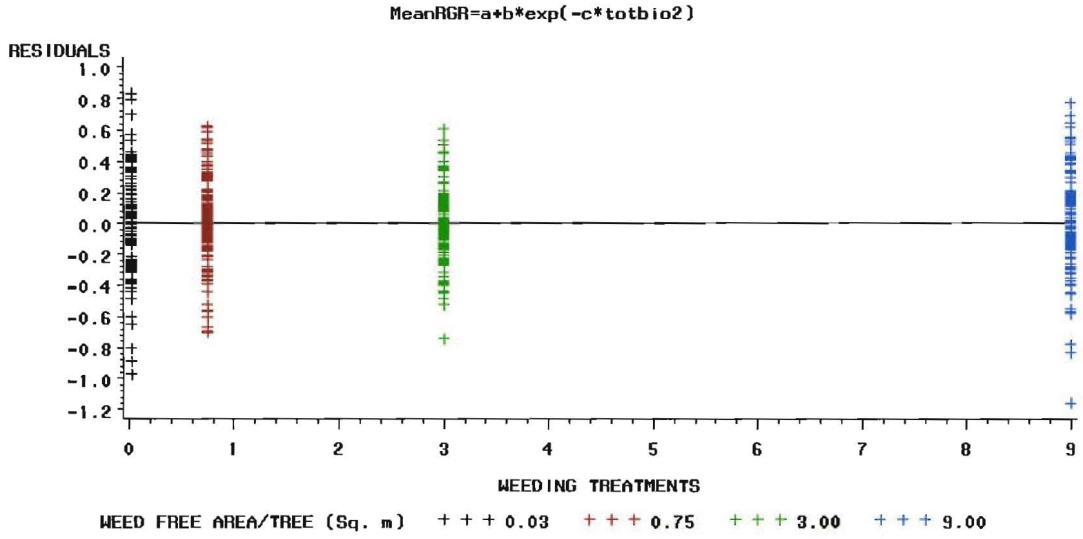

Figure 6.12: Plot of residuals versus weeding treatments.

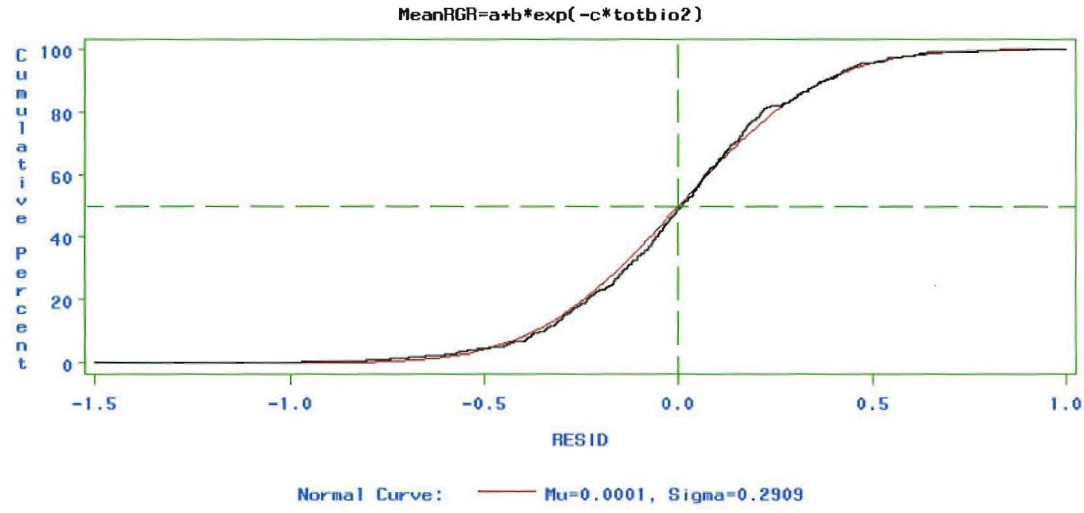

Figure 6.13: Normal curve of residuals for relative growth model.

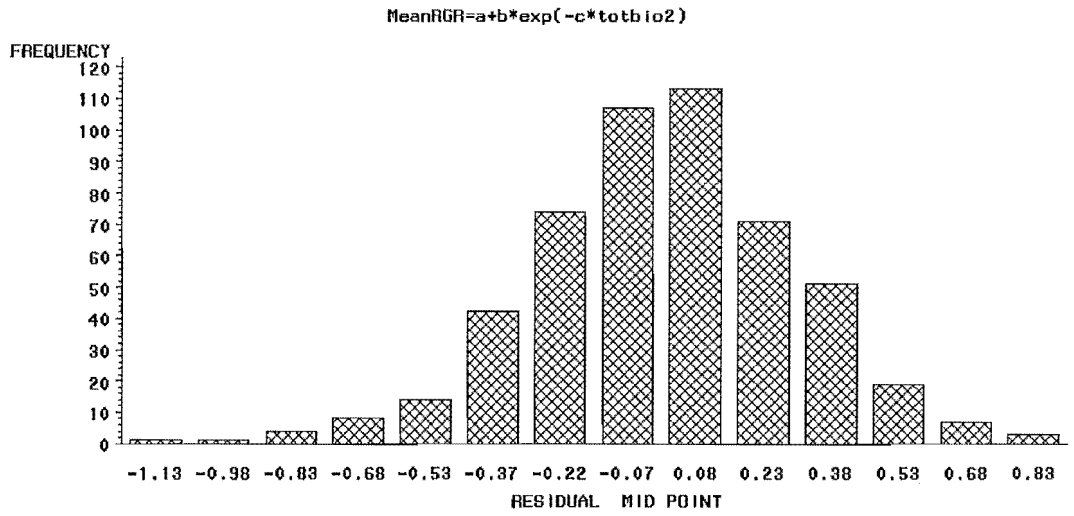

Figure 6.14: Frequency distribution of residuals for relative growth rate model.

The coefficients from the fits were plotted to show $\overline{RGR}$ changes with tree size for each weeding treatment (Figure 6.15). The trends showed that trees in Wc3 had a deeper curvature than trees in Wc9 while those in Wc0.75 had a lower asymptote. Trees in Wc0.03 had a positive curvature while all the other treatments had a negative (concave) curvature. Allowing for changes in ULR and LAR (using RGR expansion) increased RGR. However, Wc0.75 had mixed results showing a more pronounced fall in RGR with increasing size (Figure 6.16). Weighting for leaf efficiency resulted in minute changes only.

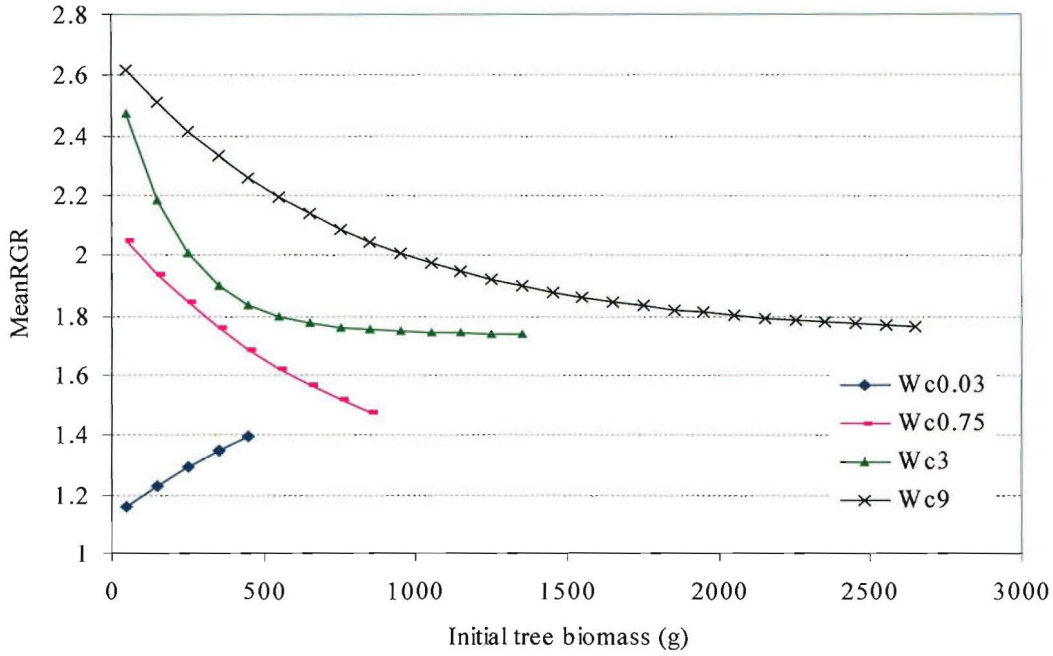

Figure 6.15: Total tree $\overline{RGR}$ trends with increasing initial tree biomass (g) for each weeding treatment.

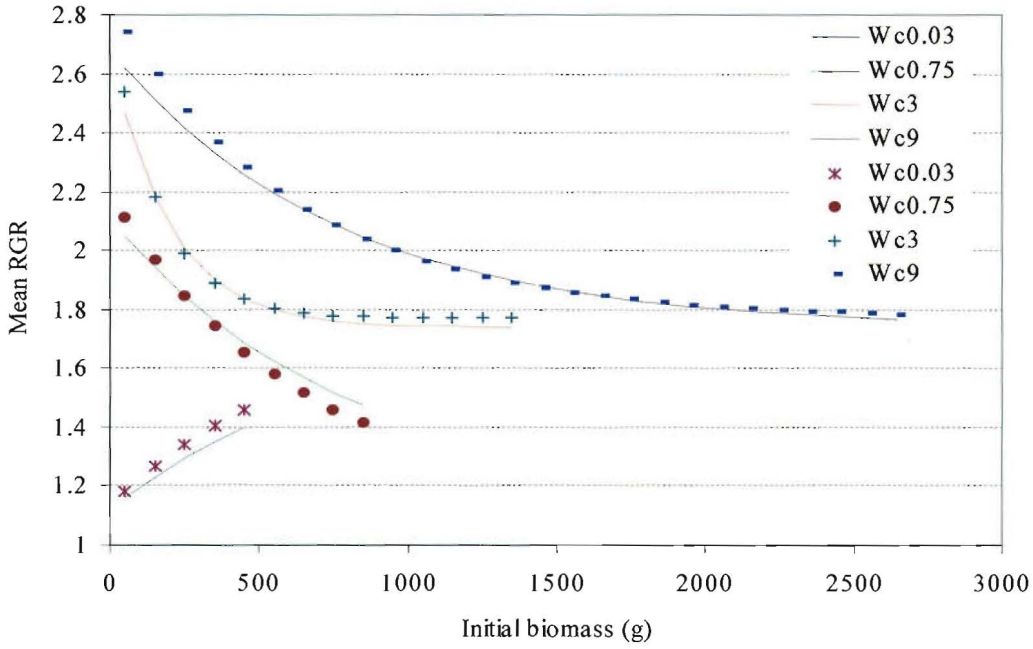

Figure 6.16: Comparison of total tree $\overline{RGR}$ trends with (symbols) and without weighting (continuous lines) vs. initial tree biomass (g) for each weeding treatment.

6.5.2 Explaining the changes in mean RGR using unit leaf rate, specific leaf area, leaf weight ratio and leaf area ratio

6.5.2.1 Mean Unit leaf rate (ULR)

Mean Unit leaf rate decreased with tree age and size in all the weeding treatments but the control (Figures 6.17 and 6.18). Mean Unit leaf rate decreased with increasing weed competition in all three clones during age 2 (Figure 6.18). However, during age 3 there was an increase in ULR for clone 3 between Wc3 and Wc0.03. Mean ULR decreased with time in Wc9, Wc3 and Wc0.75 for clone 3, but increased in Wc0.03. For clone 1, ULR decreased with time in Wc9 and Wc3 but increased in Wc0.75 and Wc0.03, while clone 2 showed an increase in Wc9, Wc0.75 and Wc0.03 (Figure 6.18). Clone 3 had a deeper curvature for mean ULR versus predicted foliage unlike the other 2 clones (Figures 6.19, 6.20,6.21).

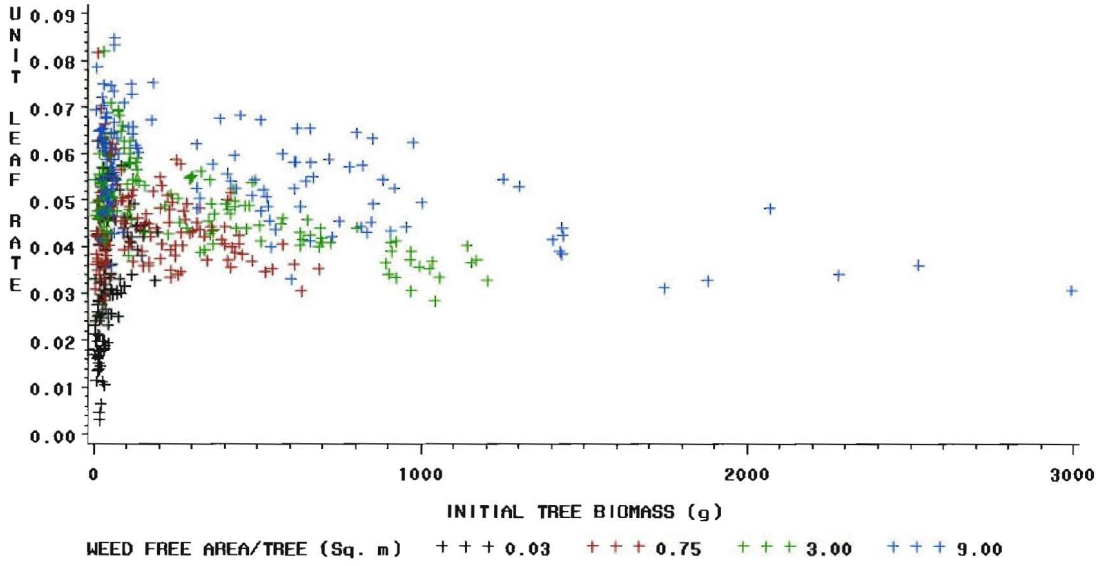

Figure 6.17: Unit leaf rate variation with initial tree size.

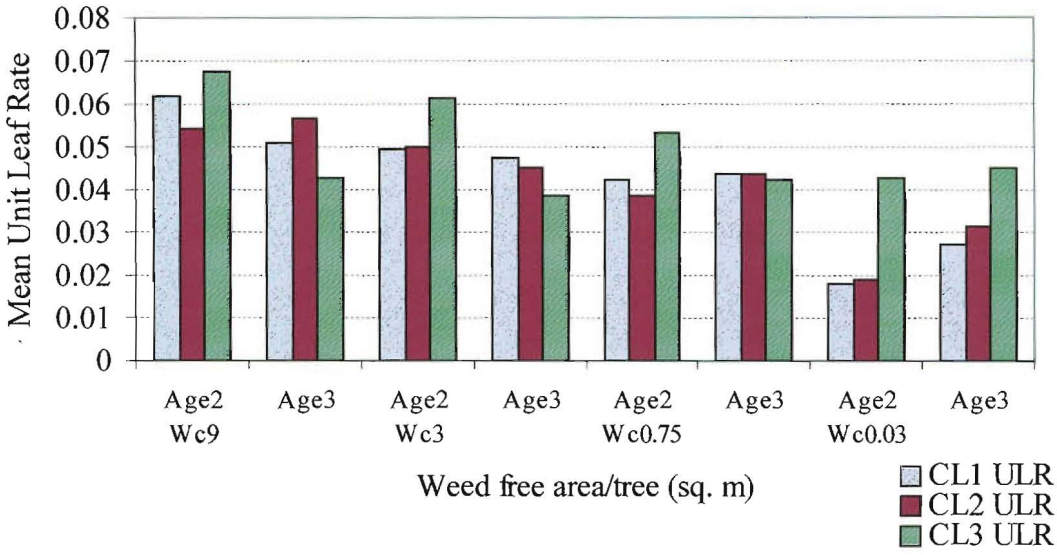

Figure 6.18: Changes in ULR by weed competition during age 2 and 3 for clones 1, 2 and 3.

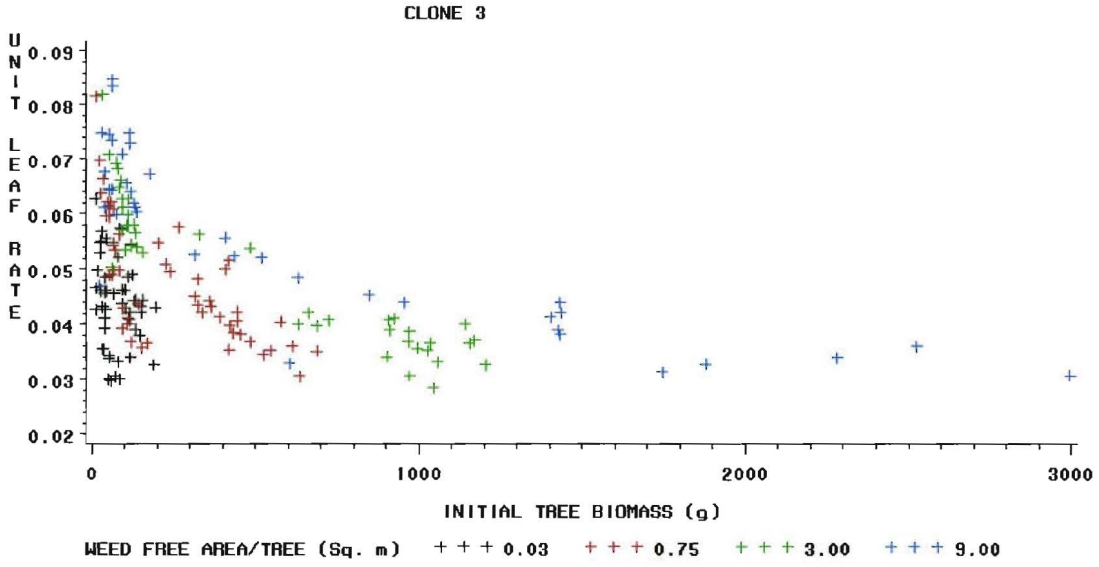

Figure 6.19: Unit leaf rate change versus initial size for clone 3.

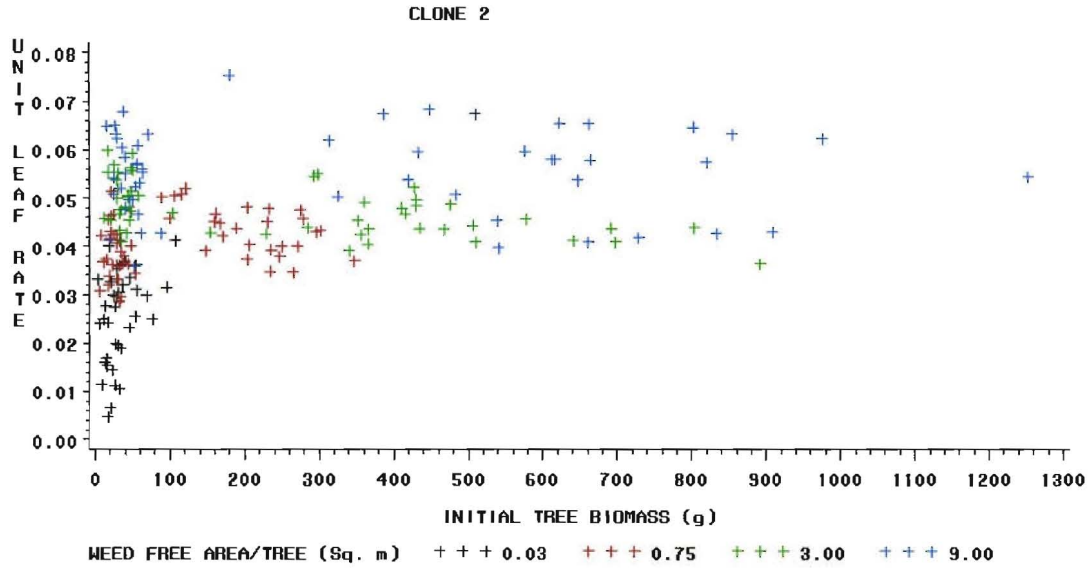

Figure 6.20: Unit leaf rate change versus initial size for clone 2.

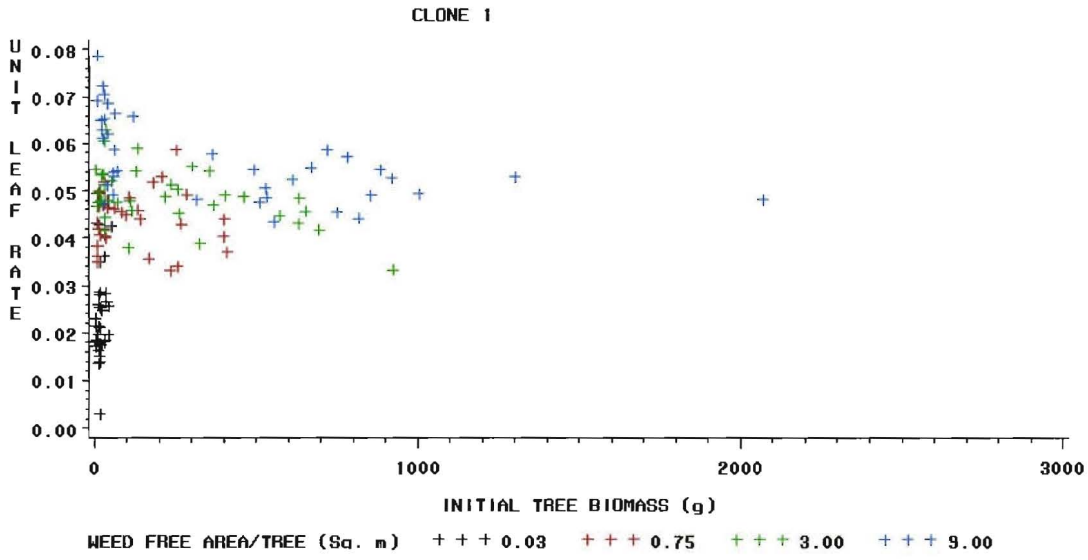

Figure 6.21: Unit leaf rate change versus initial size for clone 1.

6.5.2.2 Specific leaf area (SLA)

Specific leaf area decreased with both time and tree size (data not shown). Specific leaf area was significantly lower for trees growing in weedy plots compared to the other treatments which did not differ significantly amongst each other (Figure 6.22). Meanwhile there were no significant differences in specific leaf areas among the 3 clones.

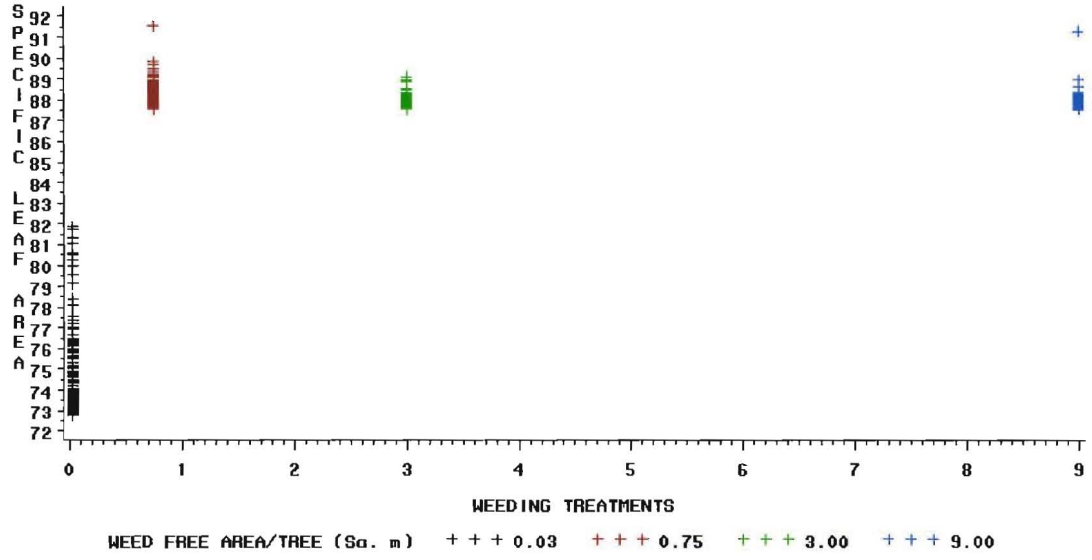

Figure 6.22: Specific leaf area variation with weed competition.

6.5.2.3 Leaf weight ratio (LWR)

Leaf weight ratio increased with increasing initial tree size in clone 3 while the opposite was true for clones 1 and 2 (Figure 6.23).

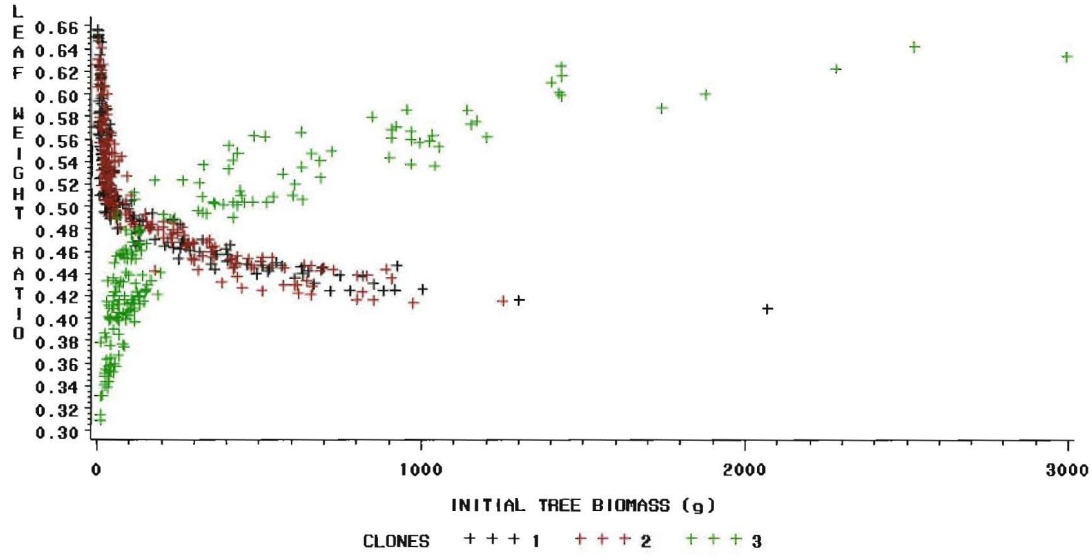

Figure 6.23: Leaf weight ratio versus initial tree biomass for clones 1, 2 and 3.

Clone 3 showed an increase in LWR with increasing weed free area per tree as well as from age 2 to 3 (Figure 6.24). However, clones 1 and 2 showed a decrease in LWR with increasing weed free area per tree as well as from age 2 to 3 (Figure 6.25).

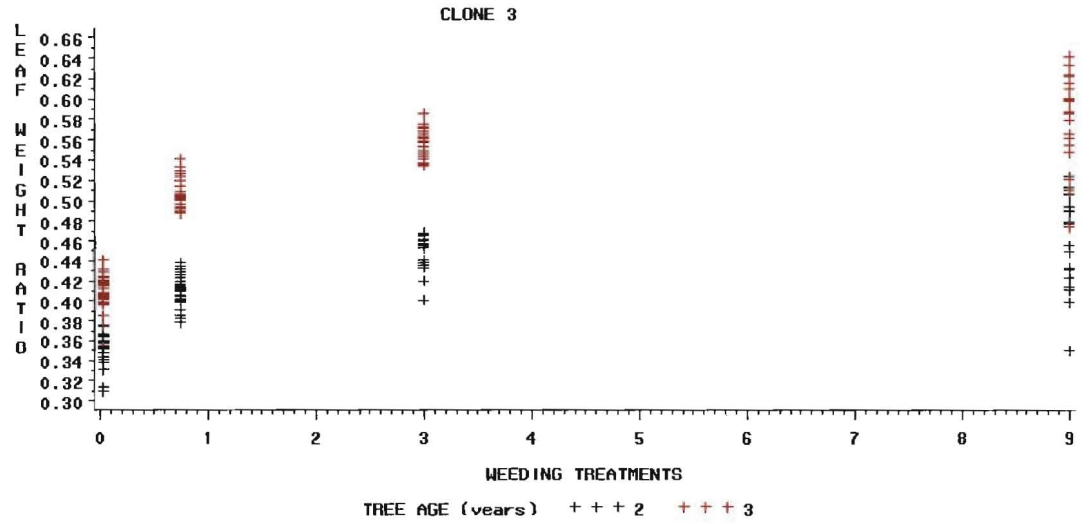

Figure 6.24: Leaf weight ratio variation with increasing weed free area per tree (sq. m) at ages 2 and 3 for clone 3.

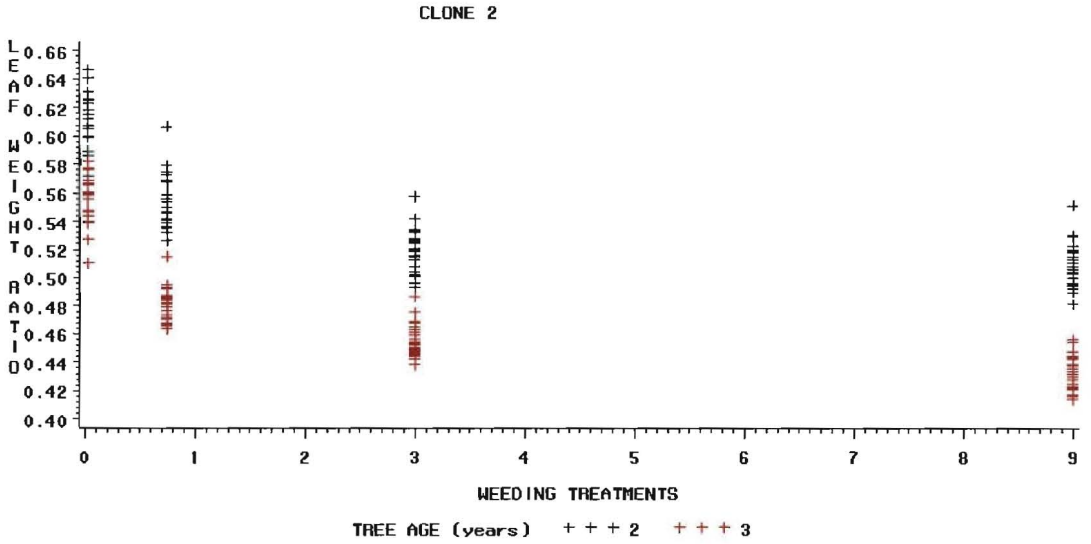

Figure 6.25: Leaf weight ratio variation by increasing weed free area per tree (sq. m) at ages 2 and 3 in clone 2 (a similar relationship for clone 1 is not shown).

6.5.2.4 Leaf area ratio (LAR)

Mean leaf area ratio increased with tree age in clone 3 but decreased with age in clones 1 and 2. A similar trend was shown when LAR was plotted against initial tree biomass (Figure 6.26). Trees growing with weeds had the lowest LAR. Clone 3 had a unique trend compared to the other 2 clones (Figures 6.27, 6.28).

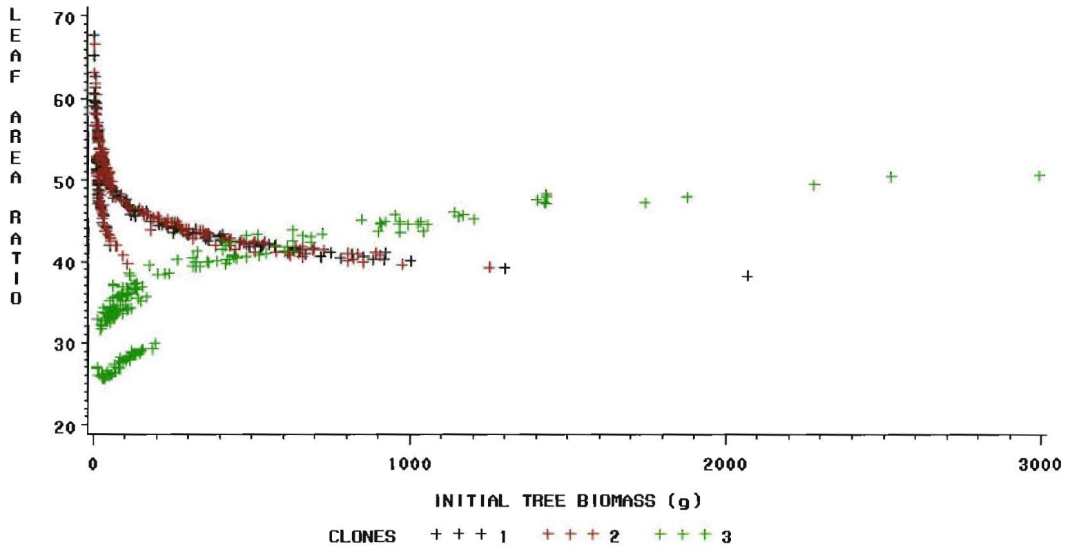

Figure 6.26: Mean leaf area ratio versus initial tree biomass (note the lower values shown by Wc0.03 = lower short curves).

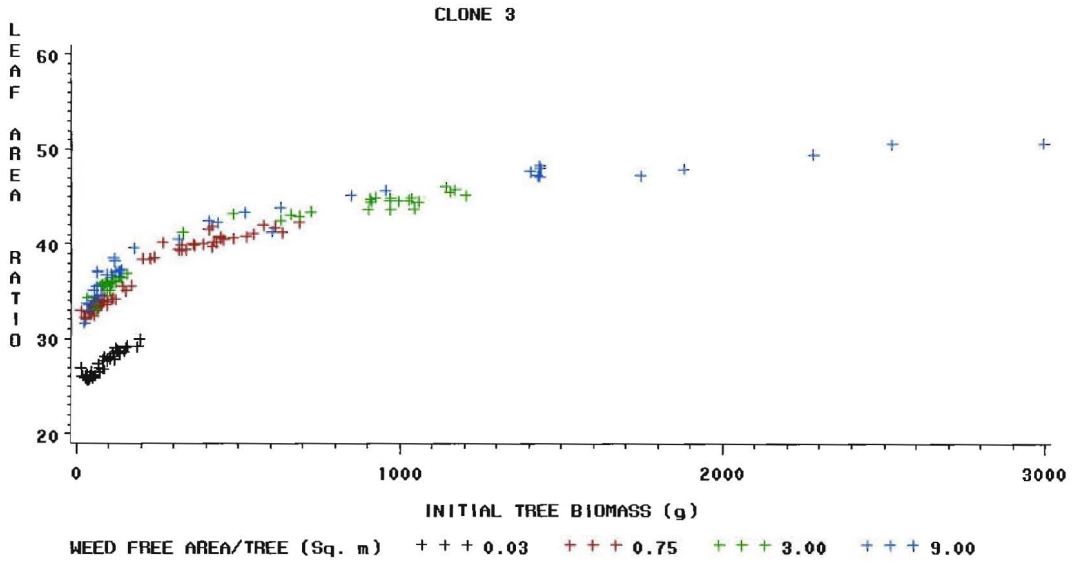

Figure 6.27: Mean leaf area ratio variation versus initial tree biomass (g) for clone 3.

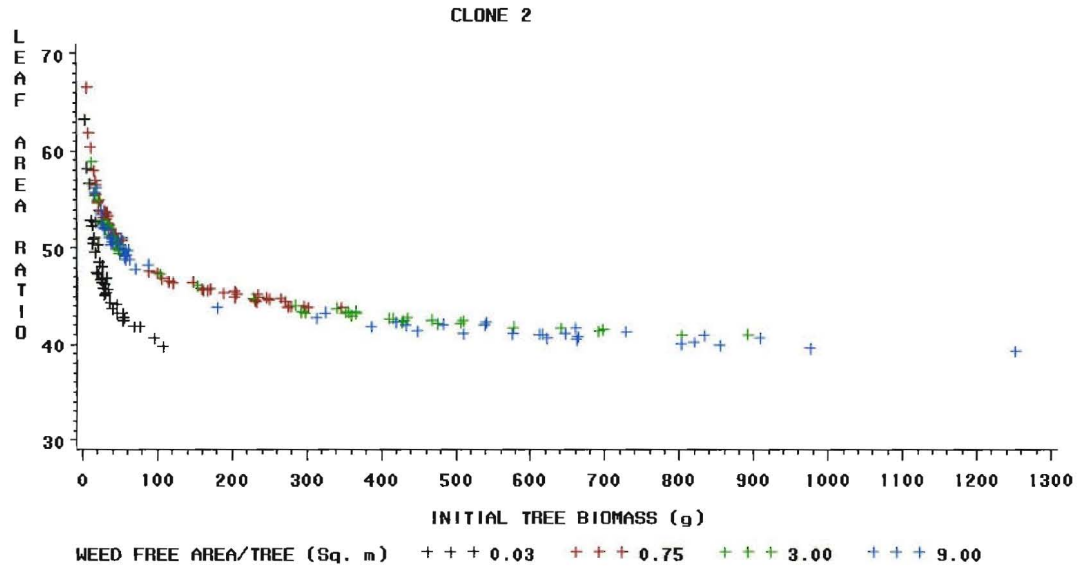

Figure 6.28: Mean leaf area ratio variation versus initial tree biomass (g) for clone 2 (a similar relationship for clone 1 is not shown).

Clone 3 showed a strong trend of increasing LAR with increasing weed free area per tree (Figure 6.29). However, clones 1 and 2 had a weaker trend (Figure 6.30).

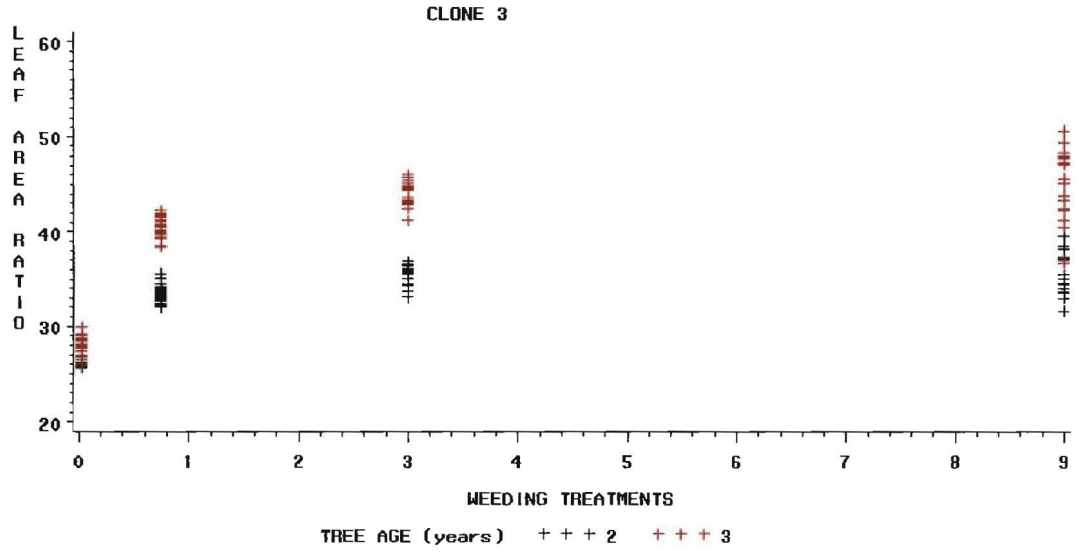

Figure 6.29: Mean leaf area ratio variation with increasing weed free area per tree for clone 3.

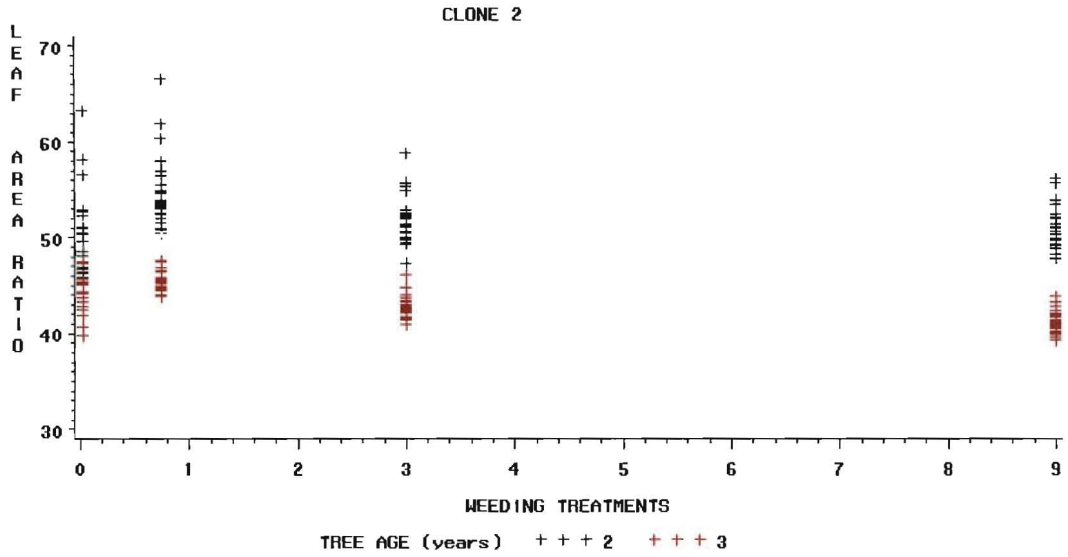

Figure 6.30: Mean leaf area ratio variation with increasing weed free area for clone 2 (similar relationship for clone 1).

6.6 DISCUSSION

According to Blackman (1919) RGR would be constant provided that assimilation rate per unit leaf area (ULR) remained constant and/or leaf area ratio (LAR) remained constant. These assumptions were clearly breached by the trees in this study. Trees changed their allometic ratios following changes in leaf weight ratios in the third growing season. Net assimilation ratios did not keep pace with increases in leaf weight to maintain constant ratios.

Trees growing in weed free micro-environments (Wc9, Wc3 and Wc0.75) had generally higher mean RGR than their counterparts in the control plots. The low RGR of trees in the control could have been due to low LA and hence photosynthetic capacity leading to low net assimilation rates. Trees in the control had low ULR which together with low LAR resulted in low overall mean RGR. Trees in the control had also more older less efficient foliage (Chapter 5 part II). This definitely affected their overall C-fixation capacity and hence their RGR.

Mean relative growth rate decreased with time and size in all weeding treatments but the control. The increase in mean RGR in Wc0.03 was most likely due to the following;

1) an increase in ULR with age (Figure 6.31) as a result of seasonal weather effects (see 2 below),
2) increased photosynthetic activity in the 3rd growing season due to favourable weather compared to the previous season (year 2 - Kirongo and Mason 1999), and
3) less likelihood of self shading as the trees had sparse crowns (less foliage).

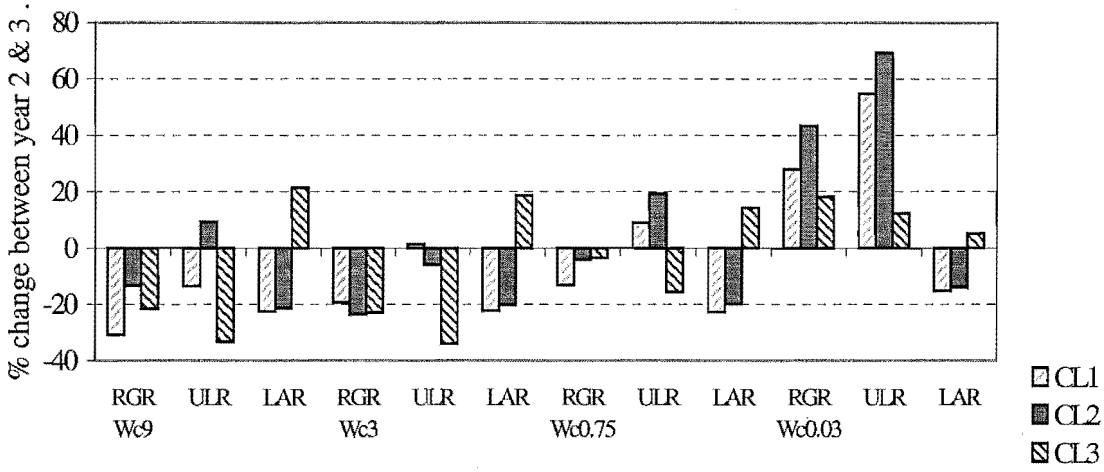

Figure 6.31: Percent changes in mean relative growth rate, unit leaf rate and leaf area ratio for clones 1, 2 and 3 vs. increasing competition between year 2 and 3.

The decrease in mean RGR with tree size and age in Wc9, Wc3 and Wc0.75 was most likely due to increases in LA, which were not immediately followed by similar increases in stored assimilates. This affected the allometry of the plants considerably. Moreover, increased foliage production during the third growing season also resulted in higher proportions of physiologically younger foliage. While this was favourable for future growth, it did not offer immediate benefits to the trees in terms of increased net assimilation rates (ULR). What's more the increases in new foliage may possibly have led to some self-shading with the result that some of the inner foliage was less effective as a producer of dry matter.

From Figure 6.31 it can be seen that changes in both ULR and LAR contributed to reductions in mean RGR for trees in weeded treatments. For example, trees in clone 3 had big reductions in ULR followed by big increases in LAR (but of a smaller magnitude compared to ULR). This resulted in moderate reductions in mean RGR. In contrast, clone 1 had small reductions in ULR (or additions in Wc3 and Wc0.75) followed by big reductions in LAR with the result that RGR declined greatly. Clone 2 showed intermediate trends.

Partitioning RGR into leaf area ratio and unit leaf rate showed that decreases in RGR were chiefly due to the following reasons.

1) Reductions in unit leaf rate (ULR) with tree age and size which were not balanced by high leaf area ratios (Figure 6.31). This is in agreement with Blackmann's (1919) postulates that for increased efficiency trees needed to have high ULR or high LAR or both. Trees in the control had very high ULR which were sufficient to increase their RGR with tree size and age.
2) Changes in allometry due to increased leaf weight during the second growing season (Figure 6.32). The increased current season leaf area should be beneficial in the future. However, in the short term the growing leaf area depends on the stored assimilates for its development (Dale 1982). This may explain in part why large additions in LA were followed by decreases in net assimilation rates (e.g. clone 3).
3) Physiological age differences of the trees due to differences in the amount of new foliage. Trees in weeded plots had higher proportions of physiologically younger foliage (e.g. Menzies *et al.* 1991). The contribution of this new foliage is expected to be evident in the next season.
4) Self-shading (Britt *et al.* 1991) as a result of the increased amounts of new foliage. Xu (2000) showed significant self-shading in 5-year old radiata pine clones. However, researchers need to be aware that RGR has been reported to decrease even in circumstances where self-shading is inconsequential, for example in seedlings (e.g. South 1991). Therefore, further studies on light conditions within the canopies of 3-year old or younger radiata pine are needed.

Mean RGR decreased with tree size and age for all the 3 clones studied in all the three weeded treatments except in the control, Wc0.03. Clone 3 had a much lower mean RGR than the other two clones in all weeded plots. This may have been due to clone 3 showing a different growth and above ground allocation strategy to the other two clones. The leaf area ratio of clone 3 increased with age and size unlike in clones 1 and 2 where it fell (Figure 6.31). However, this did not offset the acute fall in ULR in clone 3 which lowered its overall RGR considerably below those of clones 1 and 2. Therefore, the massive increases in new leaf area (3rd growing season) and hence crown size led to a decrease in clone 3's RGR.

The fall in ULR for clone 3 but not clone 2, for example, may point to the fact that clone 3, due to its massive new foliage, spent more photosynthate nurturing the young developing leafage than the latter. While high amounts of foliage promised high growth, this did not guarantee that sufficient growth would actually take place and in the way foresters envisaged (i.e. height and diameter growth). In fact more foliage could lead to severe stress during unfavourable weather (e.g. drought) a very real possibility in a dry site such as Dunsandel.

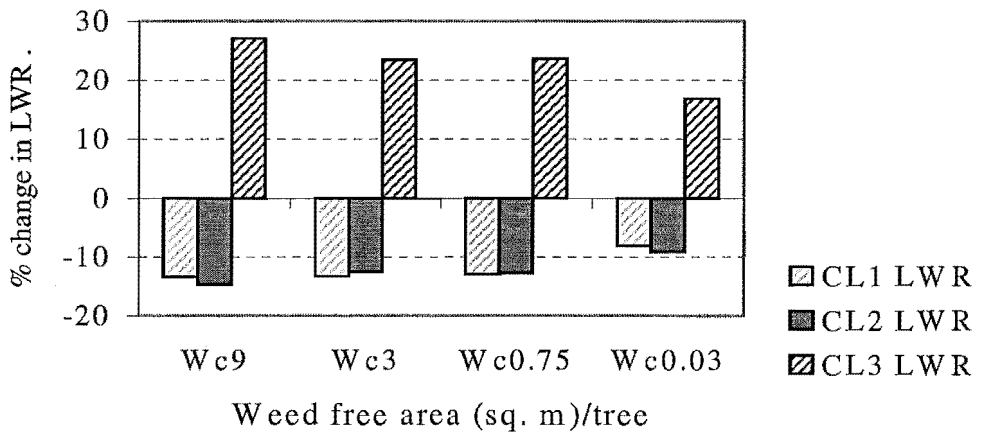

Figure 6.32: Percent changes in leaf weight ratio for clones 1, 2 and 3 vs. increasing competition between year 2 and 3.

In summary, RGR was highly influenced by ULR, which depended on the foliage amounts and the proportions of each leaf age class present. High LAR (or leaf weight ratios) did not necessarily increase RGR, unless ULR was also high. Thus changes in allometry due to increased foliage amounts had significant influences on RGR through their positive effect on leaf area and/or negative effects on PAR use efficiency possibly due to increased self-shading.

Of tree age and size, it appears that changes in tree size were more highly correlated with changes in RGR. The decrease in RGR in clone 3 following weighting for leaf efficiency in contrast to clones 1 and 2 may point at differences in crown structure, an aspect which may need investigating further. It is possible that clone 3 was already incurring significantly more self-shading than clones 1 and 2. This is a conjecture which needs following up in future studies.

6.7 CONCLUSIONS

This study has clearly demonstrated that tree growth analysts and modellers who fit models of RGR with the assumption that RGR is constant are in error. By quantifying the terms of the RGR expansion it was shown beyond reasonable doubt that both ULR and LAR changed with time and particularly with tree size, and with them RGR as well. Water-stressed trees growing in weedy plots had low absolute RGR values. However, they had increased RGR with time and size due to their high ULR. Unit leaf rate was the single dominant factor influencing RGR change in the 2- and 3-year old plants studied.

The following conclusions were drawn.

1. The $RGR = k$ model was biased with age and in particular tree size.
2. RGR decreased with size and age for trees in weeded environments but increased with size and age for trees in the control plots.
3. Weighting the leaf area of the various leaf age classes by the PAR use efficiency slightly increased RGR values of trees in clones 1 and 2 but decreased those of trees in clone 3.
4. Quantifying the terms of the RGR expansion showed that the decline in RGR was mainly due to reduced unit leaf rate (ULR).
5. Of tree age and size, the latter had more influence on RGR change than the former.
6. Clone 3 had a different growth and above-ground allocation strategy to clones 1 and 2 which made it have a lower absolute RGR compared to clones 1 and 2 but higher growth rates due to its large size.

CHAPTER 7

GENERAL DISCUSSION

This study was set up with the main aim of determining annual crown foliage budgets and hence to elucidate the probable causes for the decline in relative growth rate in juvenile trees which were free growing.

The study used a 'hybrid' approach integrating the more traditional 'empirical' methods with 'process' level data to characterise the growth responses of juvenile radiata pine clones subjected to varying weed occupancy levels.

Gathering reliable data for mechanistic models of crown production is a painstakingly labourious and costly exercise; sentiments echoed by other researchers (e.g. Landsberg 1986, Beets and Whitehead 1996), and is also intrusive killing the very subjects under study. Thus future observations cannot be directly related to the same organisms. Moreover, for canopy production models to be attractive as management tools, cost effective and reliable methods of data collection are needed. Image analysis obviates the need for destruction of subject trees.

With the availability of powerful data gathering, retrieval and manipulation tools (i.e. computers) however, there is great potential for using canopy production models and integrating them with appropriate DSS to produce reliable and biologically meaningful decision-making tools to aid managers and foresters establishing radiata pine crops. The findings from this study, therefore provide a framework and a datum for the characterisation of juvenile tree growth responses to resource deficits in terms of changes in the actual driving variables in the growth processes (i.e. leaf area).

In this study, crown areas on photographs were used successfully as surrogates for total tree biomass and leaf area. Using leaf area estimates was advantageous because leaf area is more sensitive to resource dynamics than height or diameter.

While 'empirical' models of height and diameter are the main tools used by managers, the findings from this study show the benefits which can accrue by 'marrying' the more traditional 'empirical' approach with a 'process' approach ultimately leading to some form of a hybrid model. While this study was not meant to develop a hybrid model, it has set a foundation to achieve this goal. For this to be realised, further refinements are needed and these have been itemised in the recommendations section of this chapter.

The major findings of this research were presented and discussed in chapters 4 through 6. The present section is dedicated to put the whole picture together by first revisiting the main study objectives of the research and how these were met. Thereafter the challenges for future similar studies are highlighted.

7.1 MEETING THE OBJECTIVES

This research had the following four objectives.

1. Use image analysis and fascicle monitoring techniques to quantify annual crown foliage budgets in young radiata pine as functions of tree age and size, varying weed competition levels, genotype and their interaction.
2. Quantify changes in the relative growth rate (RGR) expansion terms to shed light as to why RGR diminishes with time or size in young crops before canopy closure.
3. Determine whether or not the "rich-kid" effect is a result of genotype-by-competition interaction.
4. Develop provisional models of juvenile radiata pine tree growth and survival incorporating varying competition gradients and genetics to assist managers who

need to make informed decisions about weed control systems and clonal selection.

All the four objectives were satisfactorily met. What's more part of the study pertaining to objective 3 successfully underwent peer review and was published in a journal of international repute (see Appendix for a reprint). Moreover, two conference papers were presented; one at an international meeting in Canada and the other to a local audience in New Zealand. The summaries of these have been appended. A fourth paper was submitted for peer review in the journal of Forest Ecology and Management.

7.1.1 Objective 1: Quantifying annual crown foliage budgets

Annual crown foliage budgets were quantified for 3 of the seven clones using regressions developed from limited destructive sampling and image analysis techniques.

One of the biggest problems in getting reliable data has been the costly nature of gathering biomass data. This study has clearly demonstrated that image analysis techniques coupled with limited destructive sampling procedures can give reliable leaf area and tree biomass estimates. In this study it was also revealed that differences in height and diameter growth emanate from differences in fundamental processes of assimilate production. While this was known, relevant data especially pertaining to juvenile radiata pine "the jewel of the New Zealand plantation forestry" was scarce. In future it may be possible to integrate canopy production models into present DSS (e.g. that by Mason 1992) and make them into stronger decision support tools for foresters establishing radiata pine crops in Dunsandel and New Zealand. However, more work needs to be done before this stage is reached.

Another important finding from objective 1 was the fact that crown leaf area losses can now be quantified accurately and reliably in 3-year old radiata pine trees. Hitherto leaf area losses were estimated from litter fall needles, incurring some

considerable error and bias (Raison *et al.* 1992). In this study leaf area losses were calculated by counting actual needle survival in the crowns. The results and experience gained serve as an invaluable datum for future leaf area balance models.

7.1.2 Objective 2: RGR decline with age and size

Trees are known to show a decline in relative growth rate (RGR) with age and size, a fact which has led to conflicting use and interpretation of RGR calculations (South 1991). While the reasons for the decline in RGR were postulated by Blackman (1919) (see Chapter 6) and by other researchers in the recent past (e.g. Menzies *et al.* 1991, Britt *et al.* 1991) actual data to investigate these conjectures have been scarce. Mason *et al.* (1996a) suggested modellers use functions which allowed RGR to vary with size; $\frac{dY}{dt} = \alpha Y^{\beta}$ (7.1).

In this study the reasons why RGR declined with age and size in young trees which were free growing were presented. The study has reliably dissipated the notion of a 'constant RGR' removing size related differences and has shown beyond reasonable doubt that RGR changes were governed by unit leaf rate (ULR) and size related factors. For example, trees with high foliage addition rates changed their LWR, LAR and allometry. Increases in the amount of foliage resulted in increased RGR only if the increased foliage led to increased ULR or if the increases in LAR were large enough to counter low ULR.

Trees in the unweeded control treatment showed increased RGR with size and time because of small overall changes in allometry coupled with high ULR. This came at a price, however; reduced overall growth due to low leaf areas.

This study demonstrated that researchers and managers can gain more insights about the outcomes of their decisions if they think in terms of the effects of their actions to the production processes of the tree. For example controlling weeds is an expensive silvicultural operation. However, the decision not to control, notwithstanding its

immediate advantages on the balance sheet, results in trees which have less efficient canopies with higher proportions of older foliage. Regarding the question of complete weeding or not the study used a variation of control options to offer flexibility as well as practicability in case managers opted to leave some weeds in the site. These alternatives are very important to the industry especially given the increasing public concerns regarding minimising chemical use in forests.

7.1.3 Objective 3: The "Rich-kid" effect

Trees growing in weed-free micro-environments made good use of the improved growing conditions and no rich-kid effect was observed. An in depth analysis showing the absence of the rich-kid effect was conducted by Mason and Kirongo (1999) and a reprint of this paper is attached in the appendix. Trees in weed free micro-environments had significantly higher height and GLD growth than those in the controls. Increased height growth is beneficial and ensures that trees are less likely to be affected by frosts (Menzies and Chavasse 1982). Trees with vigorous height and GLD growth also compete better for light (Mason 1992, Richardson 1993). In this study clone 3 had more rapid height growth than the other 2 clones studied in depth.

7.1.4 Objective 4: Provisional height, basal-basal area and survival models

The results from this study made it clear that significant benefits or growth differences occur in juvenile clones contrary to common belief that significant differences became noticeable after canopy closure (e.g. Burdon 1995). This study has shown clearly that clonal benefits can be significant even at an early age of 3 years. While these findings are directly applicable to Dunsandel, these observations serve to whet the appetite for similar studies in other areas in New Zealand where radiata pine grows. What's more, trends from the model coefficients clarified that

managers do need to site match their clones in Dunsandel and elsewhere. For managers in Dunsandel the results point out clearly that clones 1 and 5 may offer unstisfactory growth.

The use of genetically modified organisms (currently the clones used in forest plantations do not fall into this category) is viewed by some concerned citizens and scientists as a 'double-edged sword'; bringing benefits to the industry but with potential dangers (unethical, future performance not guaranteed, possible contamination of native species). These concerns are acknowledged and should be treated as an impetus for breeding research as mentioned by others (e.g. Ahuja and Libby 1993a,b, Mullin and Bertrand 1998, Burdon 1999).

7.2 RECOMMENDATIONS

A reasonable amount of work in this study focused on quantifying fascicle growth dynamics and mortality both spatially and temporally. Given that we now have some information on actual needle losses, it may pay in future to take detailed light measurements and to undertake sensitivity analyses to test different assumptions regarding the finer details of needle mortality in simple ways which can be easily integrated in to available C-fixation models of young radiata pine. Thus, while detailed knowledge of mortality patterns (both spatial and temporal) may not be of immediate benefit to forest managers, such studies increase our knowledge and broaden our understanding of the crown growth processes and could be useful in increasing sensitivity of current leaf area balance models.

To make the work started in this project bear fruits the following topics need further research.

1. Allocation patterns to below ground structures as functions of variable weeding treatments and genotype.
2. Leaf area losses with short time intervals (2 weeks) during the main growing season so as to improve the reliability and sensitivity of the current outputs.

3. Canopy characterisation and photosynthesis measurements and within crown self-shading in trees growing under variable weed occupancy. Xu (2000) did similar work on 5-year old radiata clones but lacked data on variable weeding treatments.
4. Leaf area growth dynamics incorporating nutrition and water use models by the trees.

Studies on some of these aspects are already underway notably the ongoing project undertaken by Mike Watt (Ph. D. student at the School of Forestry, University of Canterbury). The findings presented in this thesis and those by Xu (2000) and later by Mike Watt could in future be integrated with a DSS (such as that developed by Mason (1992)) to aid managers making decisions regarding the establishment of young crops of radiata pine in Canterbury, New Zealand.

CHAPTER 8

SUMMARY AND CONCLUSIONS

8.1 SUMMARY

Image analysis techniques, foliage monitoring (leaf area spatial distribution, needle mortality in space and time) and limited destructive sampling methods were used to estimate crown foliage budgets of 3 radiata pine clones growing under variable pasture competition during the first three years of establishment.

Results suggest why trees growing with weeds may not be able to take full advantage of future favourable growing conditions, and these have been highlighted.

Trees growing with weeds had low canopy production rates which were related to reduced moisture availability.

Mean relative growth rate ($\overline{RGR}$) increased with age and size for trees in the control, Wc0.03, treatment but it decreased with age and size in all the weeded treatments (i.e. Wc0.75, Wc3 and Wc9). $\overline{RGR}$ rose steadily with increasing weed free area per tree with trees in Wc0.03 showing the lowest values. Clone 3 had lower $\overline{RGR}$ than the other 2 clones studied.

Quantifying the RGR expansion terms and allowing for variation in these terms;

$$RGR = \underbrace{\frac{dW}{dT}\frac{1}{LA}}_{ULR} * \underbrace{\frac{LA}{Lw}}_{SLA} * \underbrace{\frac{Lw}{W}}_{LWR} \qquad (8.1)$$

(SLA = specific leaf area, LWR = leaf weight ratio, ULR = unit leaf rate) increased the curvature of the relationship between RGR and size.

Weighting the leaf area by its PAR use efficiency of the various foliage age classes did not change the decline in $\overline{RGR}$ with time and size. However, within clones weighting resulted in increased $\overline{RGR}$ for clones 1 and 2, but reduced $\overline{RGR}$ for clone 3.

Clone 3 had a different carbon allocation strategy to that shown by clones 1 and 2. Clone 3 had a high ratio of leaf weight to total tree dry weight and reduced unit leaf rate because of its high leaf area.

8.2 CONCLUSIONS

The following overall conclusions were drawn from this study.

8.2.1 Tree height and GLD growth

Competition from weeds reduced tree stem growth and above ground allocation by reducing moisture availability, delaying foliage emergence, diminishing foliage expansion and canopy growth. Suppressed trees had proportionally more 3-year-old, less efficient foliage and reduced new foliage. Weed competition therefore reduced current growth but also led to trees that were morphologically and physiologically less prepared to respond to favourable environments that might be created by, for example, weed control four years after planting or by uncharacteristically wet summer (such as the summer of 1999). The implications for long-term growth trends are increased rotation length hence risk, reduced volume and weight of fibre, and reduced profit margins.

8.2.2 Needle mortality

Needle mortality had two main components; mortality from the stem and mortality from the branches. Mortality from the branches was linearly (new terms enter equation in a linear fashion as opposed to multiplication or power form) related to genotype, genotype-by-weeding interaction, crown area and crown width. Mortality on the stem was related to proportional height, whorl numbers and crown area.

Overall needle mortality for the whole study period was related to needle age, genotype, weeding-by-clone interaction, tree position (branch or stem) and tree size (crown area, proportional height, number of whorls and distance from the edge of the crown to the sampling unit). The best overall models of needle mortality for 3-year old needles for stem and branches were:

$$Mort_{St} = 127.031 - 1.1065 * Pcht + 7.521 * Avwhl + 0.00323 * CA_2 - 0.0311 * \mathrm{Re}lCA - 0.499 * Avht \qquad (8.2)$$

$$Mort_{Br} = 25.369 + 18.9820 * CL - 1.458 * CL * Wc + 0.00953 * CA_1 + 0.05044 * \mathrm{Re}lCA \qquad (8.3)$$

where;

$Mort_{St}$ and $Mort_{Br}$ = stem and branch 3-year-old needle mortality, Pcht = proportional height, Avht = mean height during the period, Wc = weeding, CL = clones, CA1 = initial crown photo area, RelCA = relative crown photo area and Avwhl = average whorls during the period.

Trees in the control lost proportionally fewer needles than their counterparts in weeded environments. Clone 3 lost more 3-year-old needles than the other 2 clones. In general, faster growing trees lost more 3-year-old needles, but the relationship between needle losses and growth rate still differed among clones and weed control treatments.

8.2.3 Image analysis: Crown photo area, leaf area and total tree biomass

Crown area on photographs was related to total foliage dry weight by the equation;

$$Leaf\ drywt = \alpha * (Crown\ \mathrm{Im}age\ area)^{\beta} \qquad (8.4)$$

The estimated coefficient values were,

$\alpha = 1.3193 + 0.4479*V_3$ and $\beta = 1.1864 + 0.2435*V_3$.

V_3 was a dummy variable for clone 3. Residuals were within ± 0.2 kg.

For total tree biomass by crown photo area, the function and estimated coefficient values were;

$$Total\ tree\ drywt = \alpha * (Crown\ \mathrm{Im}age\ area)^{\beta} \qquad (8.5)$$

where;

$\alpha = 2.909 + 0.4256*V_3$ and $\beta = 1.276$.

Residuals of the tree biomass by crown photo areas model were within +0.4 and -0.3.

An exponential equation was found to best describe the relationship between stem biomass vs. tree volume index (GLD^2*H);

$$Stem\ biomass = (\alpha_0 + \alpha_1 * V_1 + \alpha_2 * M_1) * (GLD^2 * H)^{(\beta_0)} \qquad (8.6)$$

where;

α and β were regression coefficients and V_1 was a dummy variable for clone 1 while M_1 was a dummy variable for Wc0.75.

The coefficient values were; $\alpha_0 = 0.0008477$, $\alpha_1 = -0.00002277$, $\alpha_2 = 0.00003757$ and $\beta = 0.75301$. The model predicted stem dry weight to within -0.1003 and +0.0909 kg.

Branch biomass was modelled using a linear function;

$$Branch\ biomass = (-0.0356 + 0.07602 * Age_2) + (0.00007764 + 0.00007239 * Age_2) * (GLD^2 * H) \qquad (8.7)$$

All residual were within -0.185 to +0.144.

Changes in allometry and factors related to physiological aging caused violation of type I responses. During the 3rd growing season trees in weed free microenvironments put up a lot of new foliage and as a result recorded diverging growth trends (type II as opposed to parallel growth trends or type I). The high amounts of new foliage relative to older foliage led to changes in allometry.

8.2.4 Crown foliage budgets

Mean tree needle mortality and foliage dry weight by crown area were used to quantify tree foliage budgets over the 3 year period using the equation;

$$NewLA_{T3} = \Pr edLA_{T3} - ([\Pr edLA_{T2} - \Pr edLA_{T1}] + NetLA_{T1}) \qquad (8.8).$$

$PredLA_{T3}$, $predLA_{T2}$, $predLA_{T1}$ = predicted total tree foliage area from equations 6.28, 6.27 and 6.26 in 1999, 1998 and 1997 respectively. $NetLA_{T1}$ = net 3-year-old foliage (1997 foliage) after accounting for needle mortality.

A linear relationship was found between leaf area and leaf weight;

$$Foliage\ Area = (\alpha_0 + \alpha_1 * V_1 + \alpha_2 * M_2) + (\beta_0 + \beta_1 * V_1 + \beta_2 * M_2) * Foliage\ weight \qquad (8.9)$$

where α and β are regression coefficients and V_i and M_i are dummy variables for clones and weeding treatments respectively. The intercepts of Wc9 and Wc3 were significantly higher than those of Wc0.75 and Wc0.03, while Wc0.03 had a significantly lower slope. Clone 3 had a significantly higher intercept than the other two clones (see Table 5.2 in section 5.3.1.2).

Leaf area spatial distribution was significantly affected by crown position. Foliage in the upper half of the crown had higher leaf area values than the bottom parts of the crown.

The crown foliage budget for year 3 was given by;

$$LAB = Newfol_3 + Netfol_2 + \%Surv_1 \qquad (8.10)$$

where;

LAB = Leaf area balance of the canopy in year 3,

$Newfol_3$ = new foliage formed during the third growing season,

$Netfol_2$ = net year 2 old foliage and

$\%surv_1$ = net 3-year-old foliage after accounting for mortality.

Trees growing in weed-free microenvironments had higher budgets than their counterparts in weedy plots. Clone 3 had a much higher annual budget than both clones 1 and 2. Crown foliage budget data were useful inputs into the RGR expansion as it was possible to account for various leaf age classes and changes in allometry.

8.2.5 Relative growth rate

RGR changed little with tree age and size for the unweeded control treatment, Wc0.03, but decreased with size in all the other treatments. The curvature of the RGR vs initial size relationship calculated from the RGR expansion (equation 8.1) was much less than that derived by using simple biomass measurements.

1) RGR calculated using total tree biomass measures increased with tree age and initial tree size (biomass) for the control, Wc0.03, but decreased for Wc0.75, Wc3, Wc9; These trends were consistent whether initial leaf biomass was used or total tree biomass. The increase in RGR with tree size and time for trees in the control was due to massive increases in ULR.

2) When RGR was calculated using the quantified terms of the RGR expansion (i.e. RGR = ULR*SLA*LWR, equation 8.1) to allow for changes in these terms it:
   i) increased with age and size for the control, Wc0.03. This confirms that improved weather alleviated the moisture stress and favoured growth and increased assimilation;

ii) showed mixed trends for Wc0.75, Wc3 and Wc9, increasing initially and then decreasing with size;

3) The relationship between initial total tree biomass and RGR calculated from the quantified terms of the RGR expansion in weeding treatments Wc0.75, Wc3 and Wc9, showed increases in curvature compared to that calculated from simple biomass changes.

Both specific leaf area (SLA) and leaf weight ratio (LWR) decreased with tree size but unit leaf rate (ULR) increased. Leaf area ratio (LAR) decreased due to a fall in SLA and LWR. Absolute increases in ULR in weed free treatments were apparently not enough to cause any appreciable changes in RGR, overall. Consequently RGR decreased with increasing tree size.

SLA values for all clones decreased with tree size. LWR values decreased in clones 1 and 2 but increased in clone 3. Consequently, LAR (= SLA*LWR) decreased in clones 1 and 2 but increased in clone 3. ULR (ratio of dry weight change with time to total tree leaf area) increased in clones 1 and 2 but fell in clone 3. This resulted in higher RGR overall for clones 1 and 2 compared to clone 3.

Overall RGR values between year 2 and 3 increased for Wc0.03 but decreased for all the other treatments. The increases in RGR for trees in Wc0.03 during year 3 were partly due to favourable weather. Quantifying terms of the RGR expansion showed that SLA and LWR (= LAR) values decreased during the same period, but ULR values increased.

The $RGR = k$ model was biased with age and in particular tree size.
RGR decreased with size and age for trees in weeded environments but increased with size and age for trees in the control plots.

Weighting the leaf area of the various leaf age classes by the PAR use efficiency slightly increased RGR values of trees in clones 1 and 2 but decreased those of trees in clone 3.

Quantifying the terms of the RGR expansion showed that the decline in RGR was mainly due to reduced unit leaf rate.

Of tree age and tree size, the latter had more influence on RGR change than the former.

8.2.5.1 Effects of Weeding on RGR

SLA and LWR increased with increasing spot sizes overall, although there was an interaction with genotype (see 8.2.5.2). The control, Wc0.03, had significantly lower SLA and LWR values than the other weeding treatments in both years.

ULR values decreased with increasing competition intensity. Wc0.03 had significantly lower ULR values than the other treatments. The biggest absolute difference in values was in moving from Wc0.03 to Wc0.75.

8.2.5.2 Genetic effects on RGR

Clones 1 and 2 had significant differences in RGR (using the expansion terms) between the control, Wc0.03, and the other treatments. No such significant differences were present in clone 3.

Leaf area ratio (LAR) was linearly related to Unit leaf rate (ULR), (negative slope). This confirms that growth is strongly related to total tree LA.

Growth differences in clones were the result of differences in carbon allocation strategies. In year 2 clone 1 had the highest LAR and clone 3 the lowest. However, by year 3 the trend was reversed. Meanwhile, in both clones 1 and 2, ULR increased significantly between Wc0.03 and Wc0.75. In clone 3, however, no such significant changes in ULR were observed.

8.2.5.3 RGR and Genotype by environment interaction

A significant clone-by-competition interaction was found for height but not GLD or Crown area. However, SLA, LWR and ULR showed significant clone-by-

competition interaction effects. Therefore competition affected tree physiology and morphology differently for different genotypes.

8.2.6 The 'Rich-kid' effect

All trees receiving total weed control responded positively to their improved growing environment. Thus no 'rich-kid'-effect was evident in this study.

8.2.7 Provisional models of height, basal-basal area and survival

Provisional models of mean height, basal-basal area/ha and survival incorporating genetics and competition intensities were developed for the first 3 years to serve as a benchmark. The general form of the functions used were ;

$$\overline{H}_T = \overline{H}_0 + \alpha * T^{\beta} \qquad (8.11)$$ for mean height (residuals between -0.27 and +0.28),

$$G_{GLT} = G_{GL_{T=0}} + \alpha * N_{T=0} * T^{\beta} \qquad (8.12)$$ for basal-basal area per hectare (residuals between -105.68 and +91.47) and

$$N_2 = N_1 \exp\left(-\alpha * \left(T_2^{\beta} - T_1^{\beta}\right)\right) \qquad (8.13)$$ for mortality per hectare.

Dummy variables were used to express the effects of variable weed intensities, genetics and interactions. The final models incorporating dummy variables were;

1) Mean height model;

$$\overline{H}_T = \overline{H}_0 + (\alpha_0 + \alpha_1 * \log(Wc) + \alpha_2 * V_2 + \alpha_3 * (Wc9 * V_4) + \alpha_5 * BL_3) * T^{(\beta_0 + \beta_1 * \log(Wc) + \beta_2 * V_5 + \beta_3 * V_1 + \beta_4 * (Wc9 * V_4))} \qquad (8.14)$$

2) Basal-basal area/ha model;

$$G_{GLT} = G_{GL_{T0}} + (\alpha_0 + \alpha_1 * V_{1,2,5} + \alpha_2 * V_7 + \alpha_3 * (BL_3 * Wc9) + \alpha_4 * Wc9) * N_0 * T^{(\beta_0 + \beta_1 * Log(Wc) + \beta_2 * (Wc9 * V_3))} \quad (8.15)$$

where;

V_i denotes i^{th} clone, BL3 = block 3 and Wc = Weeding treatment, G_{GLT} = basal-basal area/ha at time T, G_{GLT0} = basal-basal area/ha at planting, N_0 = stems/ha at planting, $\overline{H_T}$ = mean height at time T, $\overline{H_0}$ = mean height at planting, T = tree age.

The variation in alpha and beta with increasing weed free area per tree was modelled using a logarithmic function; $\alpha, \beta = \delta + \gamma * \log(Trt)$ (8.16).

3) Tree survival/ha excluding intervals where no death was observed,

$$N_2 = N_1 \exp\left(-(0.12382 + 1.1479 * V_{1,2} + 0.4226 * V_2) * \left(T_2^{1.41832} - T_1^{1.41832}\right)\right) \quad (8.17)$$

where $V_{1,2}$ was a dummy variable for clones 1 and 2 growing in Wc0.03 while V_2 was a dummy variable for clone 1 growing in Wc9.

4) Logistic model for tree survival/ha;

$$p = \frac{1}{1 + \exp(-(-0.9213 + 1.8103 * Wc0.03 + 1.1183 * V_{1,3} - 0.9213 * T_1 - 1.4213 * V_4))} \quad (8.18)$$

where T_1 = initial age and other variables are as defined earlier.

5) Adjusted predicted tree survival/ha by the probability of mortality;

$$N_{adj2} = N_1 - p * (N_1 - N_{pred2}) \quad (8.19).$$

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REFERENCES

Adlard P. G. 1995. Myth and reality in growth estimation. Forest Ecology and Management. 71: 171-176.

Ahuja, M. R. and Libby, W. J. (1993a). Clonal forestry I: Genetics and Biotechnology. Springer verlag. pp. 277.

Ahuja, M. R. and Libby, W. J. (1993b). Clonal forestry II: Conservation and application. Springer verlag. pp. 240.

Alder 1980. Forest volume estimation and yield. Vol. 2- Yield prediction. FAO Forestry paper 22/2. pp. 194.

Auld, B. A. and Medd, R. W. 1987. Weeds - An illustrated Botanical guide to weeds of Australia. Agricultural research and Veterinary Center. Inkata Press, Melbourne Australia.

Auld, B. A., Menz, K. M. and Tisdel, C. A. 1987. Weed economics. Academic Press.

Bailey, R. L. and Ware, K. D. 1983. Compatible basal area growth and yield model for thinned and unthinned stands. Can. J. For. Res. 13: 563-571.

Baker, T. G., Attiwill, P. M. and Stewart, H. T. 1984. Biomass equations for *Pinus radiata* in Gippsland, Victoria. NZ. J. For. Sci. 14(1):89-96.

Balneaves, J. M. 1981. Long-term gorse and broom control. Whats' New in Forest research. No. 100. NZ FRI Rotorua. pp. 4.

Balneaves, J. M. and Zabkiewicz, J. A. 1981. Gorse control: a review. IN: Forest nursery and establishment practices. FRI symposium No. 22, 23rd- 27th March 1981, part II - establishment practices, Chavasse C. G. R. (eds.). New Zealand FRI. p. 92-105.

Balneaves, J. M. and Menzies, M. I. 1990. Water potential and subsequent growth of *Pinus radiata* seedlings: Influence of lifting and subsequent packaging and storage conditions. New Zealand For. Sci. 20(3): 257-67.

Balneaves, J. M., Skinner, M. F. and Lowe, A. T. 1991. Improving the re-establishment of radiata pine on impoverished soils in Nelson, New Zealand. IN: Long-term field trials to assess environmental impacts of harvesting. Dyck, W. J. and Mees, C. A. (Eds.). Proceedings of IEA/BE T6/A6

workshop, Florida, U. S. A. Report No. 5. N.Z. F.R.I. Bulletin No. 161. p. 137-150.

Balneaves, J. M. and Clinton, P. 1992. Weed control increases radiata pine productivity. What's New in forest research. No. 220. NZ. FRI, Rotorua.

Bandara, D. G. 1997. Ecophysiology of clonal and seedling trees of *Pinus radiata* D. Don in an agroforestry system. Ph.D. thesis, Lincoln University, New Zealand.

Beadle, C. L., Neilson, R. E., Talbot, H. and Jarvis, P. G. 1985. Stomatal conductance and photosynthesis in a mature Scots pine forest: Diurnal, seasonal and spatial variation in shoots. J. Appl. Ecol. (22): 557 - 571.

Beets, N. P. 1977. Determination of the fascicle surface area of Pinus radiata. N.Z. J. For. Sci. 7: 397-407.

Beets, P. N. and Lane, P. M. 1987. Specific leaf area of *Pinus radiata* as influenced by stand age, leaf age and thinning. NZ. J. For. Sci. 17(2/3): 283-91.

Beets, P. N. and Pollock, D. S. 1987. Accumulation and partitioning of dry matter in *Pinus radiata* as related to stand age and thinning. New Zealand J. For. Sci. 17(2/3): 246-271.

Beets, N. P. and Whitehead, D. 1996. Carbon partitioning in *Pinus radiata* stands in relation to foliage nitrogen status. Tree Physiology. 16: 131-138.

Belli, K. L. 1987. FPES: A framework for modelling the artificial regeneration system. IN: Ek, A. R., Shifley, S. R. and Burk, T. E. (Eds.). Proceedings of the IUFRO symposium on Forest growth modelling and prediction. Minneapolis, Minnesota, USDA, Forest Service General Technical Report NC-120: 361-368.

Belli, K. L. and Ek, A. R. 1988. Growth and survival modelling for planted confers in the Great Lakes region. For. Sci. 34(2): 458-473.

Benson, M. L., Myers, B. J. and Raison, R. J. 1992. Dynamics of stem growth of *Pinus radiata* as affected by water and nitrogen supply. For. Ecol. and Mgt. 52: 117-137.

Berkowitz, A. R. 1988. Competition for resources in weed-crop mixes. Altien, M. A. and Liebman, M. (Eds.). IN: Weed management in agroecosystems – Ecological approaches. CRC Press, Boca Raton, Florida. p. 89-119.

Blackman, V. H. 1919. The compound interest law and plant growth. Annals of Botany 33: 353-360.

Blake, J. I., Somers, G. L. and Ruark, G. A. 1990. Perspectives on process modelling of forest growth responses to environmental stress. IN: Process modeling of forest growth responses to environmental stress Dixon, R. K., Meldahl, R. S., Ruark, G. A. and Warren, W. G. (Eds.). Timber Press, Oregon, USA. p. 9-17.

Bollmann, M. P., Sweet, G. B. and Rook, D. A. 1986. The influence of temperatures, nutrient status, and short drought on seasonal initiation of primordia and shoot elongation in *Pinus radiata*. Can. J. For. Res. 16: 1019-1029.

Bollmann, M. P. and Sweet, G. B. 1976. Bud morphogenesis of *Pinus radiata* in New Zealand. I: The initiation and extension of the leading shoot of one clone at two sites. New Zealand J. For. Sci. 6(3): 376-392.

Bollmann, M. P. and Sweet, G. B. 1979. Bud morphogenesis of *Pinus radiata* in New Zealand. II: The seasonal shoot growth pattern of seven clones at four sites. New Zealand Jor. For. Sci. 9: 153-165.

Borghetti, M., Vendarmin, G. G. and Giannini, R. 1986. Specific leaf area and leaf area index distribution in a young Douglas-fir plantation. Can. J. For. Res. 16: 1283-1288.

Bowles, G. P. 1981. Nursery spacing and seedling quality. IN: Forest nursery and establishment practices. FRI symposium No. 22, 23rd- 27th March 1981, Chavasse C. G. R. (eds.). New Zealand FRI. p. 101-112.

Boyall, L. A. 1983. The control of perennial weeds. IN: Recent advances in weed research, Fletcher, W. W. (ed.). Common wealth Agricultural Bureaux, Gresham Press, Old woking, Surey. p. 141-170.

Brand, D. G. 1986. A competition index for predicting the vigour of planted D. fir in the South Western British Columbia. Can. J. For. Res. 16: 23-29.

Brand, D. G. 1991. The establishment of boreal and sub-boreal conifer plants: An integrated analysis of environmental conditions and seedling growth. For. Sci. 37: 68-100.

Brand, D. G., Weetman, G. F. and Fehsler, P. 1987. Growth analysis of perennial plant: The relative production rate and its yield components. Annals of Botany. 59: 45-53.

Briggs, G. E., Kidd, F. and West, C. 1920. A quantitative analysis of plant growth. I. Relative growth curve. Annals of Applied Biology. 7: 103-123.

Britt, J. R., Mitchell, R. J., Zutter, B. R., South, D. B., Gjerstad, D. H. and Dickson, J. F. 1991. The influence of Herbaceous weed control and seedling diameter on six years of Loblolly pine growth - A classical growth analysis Approach. For. Sci. 37(2): 655-668.

Brix, H. 1981. Effects of thinning and Nitrogen fertilization on branch and foliage production in Douglas-fir. Can. J. For. Res. 11:502-11.

Brix, H. 1983. Effects of thinning anf nitrogen fertilization on growth of Douglas fir: relative contribution of foliage quantity and efficiency. Can. J. For. Res. 13: 167-175.

Bruce, D. 1990. Development of empirical forest growth models. IN: Process modeling of forest growth responses to environmental stress Dixon, R. K., Meldahl, R. S., Ruark, G. A. and Warren, W. G. (Eds.). Timber Press, Oregon, USA. p.191-199.

Bruce, D. and Wensel, L. C. 1987. Modelling Forest growth: Approaches, definitions and problems. IN: Ek, A. R., Shifley, S. R. and Burk, T. E. (Eds.). Proceedings of the IUFRO symposium on Forest growth modelling and prediction. Minneapolis, Minnesota, USDA, Forest Service General Technical Report NC-120: 1-8.

Brunsden, G. J. 1981a. Box pruning trials and field results. IN: Forest nursery and establishment practices. FRI symposium No. 22, 23rd- 27th March 1981, Chavasse C. G. R. (eds.). New Zealand FRI. p. 142-153.

Brunsden, G. J. 1981b. Root development and toppling of planted trees in relation to nursery stocks, planting methods and site preparation. IN: Forest nursery and establishment practices. FRI symposium No. 22, 23rd- 27th March 1981, part II - establishment practices, Chavasse C. G. R. (eds.). New Zealand FRI. p. 272-276.

Burdon, R. D. 1995. Role of genetic improvement. Forestry Handbook - Don Hammond (ed.). New Zealand Institute of Foresters (Inc.) p. 65-67.

Burdon, R. D. 1999. Risk management issues for genetically enginnered forest trees. New Zealand J. For. Sci. 29(3): 375-390.

Burdon, R. D. and Sweet, G. B. 1976. The problem of interpreting inherent differences in tree growth shortly aftr planting. Cannell, M. G. R. (ed.). Tree physiology and yield improvement. Academic Press. London. p. 483-502.

Burkhart, H. E., Cao, Q. V. and Ware, D. K. 1981. A comparison of growth and yield prediction models for Loblolly pine. School of Forestry and Wildlife resources. Virginia polytechnic Institute and state University, Blacksburg. Publication No. FWS-2-81. pp. 59.

Burkhart, H. E. and Sprinz, P. T. 1984. A model for assessing hardwood competition effects on yield of loblolly pine plantations. School of Forestry and Wildlife resources, Virginia Polytech. Inst. and State University. Blacksburg Publ. FWS-3-84. pp. 55.

Burton, P. J. 1993. Some limitations inherent to static indices of plant competition. Can. J. For. Res. 23: 2141-2152.

Cannell, M. G. R. and Grace, J. 1993. Competition for light, measurement and quantification. Can. J. For. Res. 23: 1969-1979.

Carson, M. J. and Burdon, R. D. 1991. Relative Advantages of Clonal forestry and vegetative multiplication. IN: Proceedings FRI/NZFP Forests Ltd, Clonal forestry Workshop 1-2 May 1989, Miller, J. T. (ed.). Rotorua New Zealand. FRI Bulletin No. 160. p. 41-43.

Carson, M. J. and Inglis, C. S. 1988. Genotype and location effects on internode length of *Pinus radiata* in New Zealand. NZ. J. For. Sci. 18: 267-279.

Causton, D. R. 1983. A biologist's Basic mathematics. Edward Arnold publishers.

Causton, D. R. and Venus, J. C. 1981. The Biometry of plant growth. Edward Arnold publishers. pp. 307.

Chang, S. X.; Weetman, G. F. and Preston, C. M. 1996. Understorey competition effect on tree growth and biomass allocation on a coastal old-growth cutover site in British Columbia. Forest Ecology and Management. 83: 1-11.

Chapman, G. W. and Allan, T. G. 1978. Establishment techniques for forest plantations. FAO-Forestry paper No.8 (1978). FAO, Rome. pp. 183.

Charles-Edwards, A. D.; Doley, D. and Rimmington, M. G. 1986. Modelling plant growth and development. Academic Press. pp. 1-20, 34-70.

Chavasse C. G. R. 1980. Planting stock quality: A review of the factors affecting performance. N. Z. J. For. 25(2): 144-171.

Chavasse, C. G. R. 1981. Blanking radiata pine stands. IN: Forest nursery and establishment practices. FRI symposium No. 22, 23rd- 27th March 1981, part II - establishment practices, Chavasse C. G. R. (eds.). New Zealand FRI. p. 300-301.

Christian, N. B. 1975. Decision-making principles and cases. IN: Forest resource management. Duerr, W. A., Teeguarden, D. E., Guttenberg, S. and Christiansen, N. B. (Eds.), vol1, part 3. O. S. U. Book stores, Inc. U. S. A. p. 8-1.

Clutter, J. L., Forsten, J. C., Pienaar, L. V., Brister, G. H. and Bailey, R. L. 1983. Timber management: A quantitative approach. John Wiley and sons.

Comeau, P. G., Braumandl, T. F. and Xie, Chang-Yi 1993. Effects of overtopping vegetation on light availability and growth of Engelmann spruce (*Picea engelmannii*) seedlings. Can. J. For. Res. 23: 2044-48.

Compton, J. E. and Cole, D. W. 1991. Impact of harvesting intensity on growth and nutrition of successive rotations of Douglas-fir. IN: Long-term field trials to assess environmental impacts of harvesting. Dyck, W. J. and Mees, C. A. (Eds.). Proceedings of IEA/BE T6/A6 workshop, Florida, U. S. A. Report No. 5. N.Z. F.R.I. Bulletin No. 161. p. 151-161.

Cook, R. D. and Weisberg, S. 1982. Residuals and influence in Regression. Chapman and Hall.

Cousens, R. 1987. Theory and reality of weed control thresholds. Plant protection quarterly. 2: 13-20.

Cown, D. J. 1992. New Zealand radiata pine and D. fir: suitability for processing. New Zealand FRI Bulletin No. 168. p. 19.

Cown, D. J.; McConchie, D. L. and Young, G. D. 1991. Radiata pine wood properties survey. New Zealand Ministry of Forestry. FRI Bulletin No. 50.

Cullen, A. W. J. and Mason, E. G. 1981. The use of cultivation as an aid to forest establishment. IN: Forest nursery and establishment practices. FRI symposium No. 22, 23rd- 27th March 1981, part II - establishment practices, Chavasse C. G. R. (eds.). New Zealand FRI. p. 115-126.

Dale, E. J. 1982. The growth of leaves. Studies in Biology no. 137. Eddward Arnold Publishers.

Dale, R. W. and Todd, A. C. 1988. Using cattle to control pampas grass in maramarua and waiuku forests. IN: Maclaren, P. (ed.). Proceedings of the agroforestry symposium. Rotorua. NZFRI Bulletin No. 39: 95-103.

Dalla-Tea, F. and Jokela, E. J. 1991. Needle fall, canopy light interception, and productivity of young intensively managed slash and loblolly pine stands. Forest science. Vol 37(5): 1298-1313.

Davis , L. S. and Johnson, K. N. 1987. Forest management (3rd Edition). McGraw-Hill series.

DeLong, S. C. 1991. The light interception index: A potential tool for assisting in vegetation management decisions. Can. J. For. Res. 21: 1037-1042.

Draper, N. R. and Smith, S. 1966. Applied regression analysis. 2nd Edition. John Wiley and Sons.

Dyck, W. J., Hodgkiss, P. D., Oliver, G. R. and Mees, C. A. 1991. Harvesting sand-dune forests. IN: Long-term field trials to assess environmental impacts of harvesting. Dyck, W. J. and Mees, C. A. (Eds.). Proceedings of IEA/BE T6/A6 workshop, Florida, U. S. A. Report No. 5. N.Z. F.R.I. Bulletin No. 161. p. 163-176.

Ek, A. R. 1979. A model for estimating branch weight and branch leaf weight in biomass studies. For. Sci. 25(2): 303-306.

Evans, G. C. 1972. The quantitative analysis of plant growth. Blackwell Scientific publishers. Oxford.

Evans, J. 1992. Plantation Forestry in the Tropics: Tree planting for Industrial, social, environmental and agroforestry purposes. Second Edition. Clarendon press, Oxford. pp. 1-24, 99-121, 136-228.

Fisher, R. A. 1921. Some remarks on the methods formulated in a recent article on quantitative analysis of plant growth. Annals of Applied Biology. 79: 367-372.

Fosberg, M. A. 1990. Global change-A challenge to modelling. IN: Process modelling of forest growth responses to Environmental stress (Dixon, R. K., Meldahl, R. S., Ruark, G. A. and Warren, W. G. (eds.). Timber press Inc. p.3-8.

Fredricksen, T. S., Zedaker, S. M., Smith, D. W., Seiler, J. R. and Kreh, R. E. 1993. Interference interactions in experimental pine-hardwood stands. Can. J. For. Res. 23: 2032-2043.

Fryer, J. D. 1987. Recent research in weed management - New light on an old practice. IN: Recent advances in weed research, Fletcher, W. W. (ed.). Common wealth Agricultural Bureaux, Gresham Press, Old woking, Surey. p. 181-198.

Gadgil, R. L., Sandberg, A. M., Allen, P. J. and Gallagher, S. S. 1990. Partial suppression of pampas grass by other species at the early seedling stage. IN: Basset, C.; Whitehouse, L. J. and Zabkiewicz (Eds.). "Alternatives to chemical control of weeds. Proccedings of an International conference. Rotorua, New Zealand, July 1989. Ministry of Forests. FRI Bulletin No. 155.

Garcia, O. 1988. Growth modelling- a (Re)view. New Zealand Forestry 33(3): 14-17.

Genetics and Tree Improvement Research Field (1987)- which radiata pine seed should you use? New Zealand FRI. What's New in Forest Research No. 157. pp. 4.

Gjerstad, D. H. and Barber, B. L. 1987. Forest vegetation problems in the south (USA). IN: Forest Vegetation Management for conifer production. Walstad, J. D. and Kuch, J. P. (eds.). John Wiley and sons. p. 55-75.

Glover, G. R. and Hool, J. N. 1979. A basal area ratio predictor of loblolly pine plantation mortality. For. Sci. 25: 275-282.

Goldberg, D. E. 1996. Simplifying the study of competition at the individual plant level: Consequences of distinguishing between competitive effect and response for forest vegetation management. N.Z. J. For. Sci. 26: 19-38.

Goulding, C. J. 1986. Growth and yield models. IN: Levack, H. (Ed.). Forestry Handbook, New Zealand Institute of Foresters. p. 83-84.

Goulding, C. J. 1995. Growth and yield models. IN: Forestry Handbook - Don Hammond (ed.). New Zealand Institute of Foresters (Inc.) p. 111-113.

Grace, J. C., Jarvis, P. G. and Norman, J. M. 1987a. Modelling the interception of solar radiant energy in intensively managed stands. NZ J. For. Sci. 17(2/3): 193-209.

Grace, J. C., Rook, D. A. and Lane, P. M. 1987b. Modelling canopy photosynthesis in *Pinus radiata* stands. NZ J. For. Sci. 17(2/3):210-28.

Gregory, F. G. 1926. The effect of climatic conditions on the growth of barley. Annals of Botany. 40: 1-26.

Gregory, F. G. 1928. The analysis of growth curves - a reply to a criticism. Annals of Botany. 42: 531-539.

Harman, H. M. and Syrett, P. 1990. Biological control of broom in New Zealand. IN: Basset, C.; Whitehouse, L. J. and Zabkiewicz (Eds.). "Alternatives to chemical control of weeds. Proccedings of an International conference. Rotorua, New Zealand, July 1989. Ministry of Forests. FRI Bulletin No. 155. p. 28.

Harper, G. J., Comeau, P. G., Hintz, W., Wall, R. E., Prasad, R. and Becker, E. M. 1999. *Chondrostereum purpureum* as a biological control agent in forest vegetation management. II. Efficacy on Sitka alder and aspen in western Canada. Can. J. For. Res. 29: 852-858.

Harrington, T. B. and Tappeiner II, J. C. 1991. Competition affects shoot morphology, growth duration and relative growth rates of Douglas-fir saplings. Can. J. For. Res. 21: 474-481.

Harris, J. M. 1981. The effect of tree toppling and tree lean on wood quality. IN: Forest nursery and establishment practices. FRI symposium No. 22, 23rd- 27th March 1981, part II - establishment practices, Chavasse C. G. R. (eds.). New Zealand FRI. p. 276-277.

Hill, R. L. and Gourlay, A. H. 1990. The role of biological control in the long-term management of gorse (*Ulex europeaus* L.) in New Zealand. IN: Basset, C.; Whitehouse, L. J. and Zabkiewicz (Eds.). "Alternatives to chemical control of weeds. Proccedings of an International conference. Rotorua, New Zealand, July 1989. Ministry of Forests. FRI Bulletin No. 155. p. 26-27.

Holt, J. S. 1988. Ecological and physiological characteristics of weeds. IN: Weed management in agro-ecosystems - ecological approaches. p. 7-23.

Hunt, R. 1982. Plant growth curves: the functional approach to plant growth analysis. Edward Arnold publishers.

Hunter, I. R. 1981. Enhanced growth of radiata pine transplants after soil cultivation and fertilization application on a range of soil types. IN: Forest nursery and establishment practices. FRI symposium No. 22, 23rd- 27th March 1981, part II - establishment practices, Chavasse C. G. R. (eds.). New Zealand FRI. p. 279-290.

Hunter, I. R., Hunter, J. A. C. and Graham, J. D. 1987. *Pinus radiata* stem volume increment and its relationship to needle mass, foliar and soil nutrients, and fertiliser. NZ. J. For. Sci. 17(1):67-75.

Husch, B. Miller, C. I. and Beers, T. W. 1982. Forest mensuration (3rd Edition). John Wiley and Sons. pp. 402.

Jackson, D. S. and Chittenden, J. 1981. Estimation of dry matter in *Pinus radiata* root systems. I: Individual trees. New Zealand J. For. Sci. 11(2): 164-182.

Jackson, R. W. 1981. Factors leading to mortality and uneven growth in young plantations of radiata pine. IN: Forest nursery and establishment practices. FRI symposium No. 22, 23rd- 27th March 1981, part II - establishment practices, Chavasse C. G. R. (eds.). New Zealand FRI. p. 292-300.

Jessep, C. T. 1990. Biological control programs against nodding thistle (*Carduus nutans* L.) and Californian thistle (*Cirsium arvense* L.) in New Zealand. IN: Basset, C.; Whitehouse, L. J. and Zabkiewicz (Eds.). "Alternatives to chemical control of weeds. Proccedings of an International conference. Rotorua, New Zealand, July 1989. Ministry of Forests. FRI Bulletin No. 155. p. 25.

Johnson, D. J. 1984. A rapid technique for estimating total surface area of pine needles. For Sci. 30: 913-921.

Johnston, P. R. 1990. Fungi as potential biological agents of weeds in New Zealand. IN: Basset, C.; Whitehouse, L. J. and Zabkiewicz (Eds.). "Alternatives to chemical control of weeds. Proccedings of an International conference. Rotorua, New Zealand, July 1989. Ministry of Forests. FRI Bulletin No. 155. p. 66-70.

Kay, M. 1981. Nursery insects. IN: Forest nursery and establishment practices. FRI symposium No. 22, 23rd- 27th March 1981, Chavasse C. G. R. (eds.). New Zealand FRI. p. 78-84.

Kay, M. and Smale, M. C. 1990. The potential for biological control of *Buddleja davidii* Franchet in New Zealand. IN: Basset, C.; Whitehouse, L. J. and Zabkiewicz (Eds.). "Alternatives to chemical control of weeds. Proccedings of an International conference. Rotorua, New Zealand, July 1989. Ministry of Forests. FRI Bulletin No. 155. p. 29-33.

Kinerson, R. S., Higginbotham, K. O. and Chapman, R. C. 1974. The dynamics of foliage distribution within a forest canopy. Journal of Appl. Ecology. 11: 347-53.

King, J. L. 1966. Weeds of the world, Biology and control. Plant Science Monographs. Leonard Hill, London. pp. 520.

Kirongo, B. B. 1996. Effects of non-crop vegetation on the growth and productivity of young radiata pine. MSc. Thesis, University of Canterbury (Christchurch).

Kirongo, B. B. and Mason, E. G. 1999. Using image analysis and canopy measurements to characterise the growth and morphology of juvenile radiata pine (*Pinus radiata* D. Don) clones subjected to different weed competition levels. Wagner, R. G. and Thompson, D. G. (comp.). Third International Conference on forest vegetation management: Popular summaries. Ont. Min. Nat. Resour., Ont. For. Inst., For. Res. Info. paper no. 141: 139-141.

Kirongo, B. B., Mason, E. G. and Nugroho, A. P. (in prep.). Interference mechanisms of pasture on the growth and fascicle dynamics of 3-year old radiata pine clones (submitted to Forest Ecology and Management).

Knight, P. J. 1981. The maintenance of productivity in Forest nurseries. IN: Forest nursery and establishment practices. FRI symposium No. 22, 23rd- 27th March 1981, part I - Nursery practice, Chavasse C. G. R. (eds.). New Zealand FRI. p. 48-69.

Lambrechsten, N. C. 1992. What grass is that? DSIR Information series No. 87. Government Printes (New Zealand) Ltd.

Landsberg, J. J. 1986. Physiological Ecology of Forest Production. Academic Press.

Landsberg, J. J. and Waring, R. H. 1997. A generalized model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. For. Ecol. & Mgt. 95: 209-218.

Lanini, W. T. and Radosevich, S. R. 1986. Response of three conifer species to site preparation and shrub control. For. Sci. 32(1): 61-77.

Lawton, J. H. 1990. Biological control of plants: a review of generalisations, rules and principles using insects as agents. IN: Basset, C.; Whitehouse, L. J. and Zabkiewicz (Eds.). "Alternatives to chemical control of weeds. Proccedings of an International conference. Rotorua, New Zealand, July 1989. Ministry of Forests. FRI Bulletin No. 155. p. 3-17.

Ledig, F. T. and Perry, T. O. 1969. Net assimilation rate and growth in loblolly pine seedlings. For. Sci. 15: 431-438.

Lee, S. H. 1998. Modelling growth and yield of Douglas fir using different interval lengths in the South Island of New Zealand. Phd thesis, University of Canterbury (Christchurch), New Zealand.

Leverenz, J., Deans, J. D., Ford, E. D., Jarvis, P. G., Milne, R. and Whitehead, D. 1982. Systematic spatial variation of stomatal conductance in Sitka spruce plantation. J. Appl. Ecol. (19): 835 - 51.

Libby, W. J. and Rauter, R. M. 1984. Advantages of clonal forestry. The Forestry Chronicle. 60(3): 145-149.

Liebman, M. 1988. Ecological suppression of weed in intercropping systems. Altien, M. A. and Liebman, M. (Eds.). IN: Weed management in agroecosystems – Ecological approaches. CRC Press, Boca Raton, Florida. p. 197-212.

Linder, S., Benson, M. L., Myers, B. J. and Rainson, R. J. 1987. Canopy dynamics and growth of *Pinus radiata*. I. Effects of irrigation and fertilization during a drought. Can. J. For. Res. 17: 1157-1165.

Lowery, R. F., Lamberth, C. C., Endo, M. and Kane, M. 1993. Vegetation management in tropical forest plantations.Can. J. For. Res. 23: 2006-2014.

MacDonald, P. M. and Fiddler, G. D. 1993. Feasiblility of alternatives to herbicides in young conifer plantations. Can. J. For. Res. 23: 2015-22.

MacDonald, P. M., Mori, S. R. and Fiddler, G. D. 1999. Effects of competition on genetically improved ponderosa pine seedlings. Can. J. For. Res. 29: 940-46.

MacFadyen, E. C. R. 1998. Biological control of weeds. Anu. Rev. Entomol. 43: 369-93.

Maclaren, J. P. 1993. Radiata pine growers' manual. FRI Bulletin. No. 184. pp. 140.

Madgwick, H. A. I. 1981. Above ground dry matter content of a young close-spaced *Pinus radiata* stand. New Zealand J. For. Sci. 11(3): 203-9.

Madgwick, H. A. I. 1983a. Estimation of the oven-dry weight of stems, needles, and branches of individual *Pinus radiata* trees. NZ. For. Sci. 13(1): 108-109.

Madgwick, H. A. I. 1983b. Differences in growth and weight of genotypes of pine with special reference to clones of *Pinus radiata*. NZ. For. Sci. 13(2): 115-24.

Madgwick, H. A. I. 1993. Foliage and growth distribution within crowns of *Pinus radiata* trees. NZ. For. Sci. 23(1): 84-89.

Madgwick, H. A. I. 1994. *Pinus radiata* - Biomass, Form and Growth. H. A. I. Madgwick Publ. Rotorua New Zealand. pp. 428.

MAF 2000. Ministry of Agriculture and Forestry Statistical release March 2000. SR 16/2000.

Markin, G. P. and Gardner, D. E. 1993. Status of biological control in vegetation management in forests. Can. J. For. Res. 23: 2023-2031.

Mason, E. G. 1981. Improvement of nursery and establishment techniques. IN: Forest nursery and establishment practices. FRI symposium No. 22, 23rd- 27th March 1981, Chavasse C. G. R. (eds.). New Zealand FRI. p.186-198.

Mason, E. G. 1985. Causes of juvenile Instability in *Pinus radiata* in New Zealand. New Zealand J. For. Sci. 15(3): 263-280.

Mason, E. G. and Cullen, A. W. J. 1986. Growth of *Pinus radiata* on ripped and unripped Taupo pumice soils. New Zealand J. For. Sci. 16(1): 3-18.

Mason, E. G., Cullen, A. W. J. and Rijkse, W. C. 1988. Growth of two radiata pine stock types on ripped and/bedded plots at Karioi Forest. For. Sci.18: 287-296.

Mason, E. G. 1992. Decision support system for establishing radiata pine plantations in the Central North Island of New Zealand. Phd thesis, University of Canterbury (Christchurch), New Zealand.

Mason, E. G. 1996. Planning Forest establishment operations with a computerised Decision-support system: A case study analysis of Decision-making over a full rotation. New Zealand J. For. Sci. 26(1/2): 222-234.

Mason, E. G., South, D. B. and Zutter, B. R. 1996a. Classical growth analysis for a computer age. IN: Modelling regeneration success and Early growth of forest stands. Proccedings of an IUFRO Conference. Copenhagen, Denmark. p. 221-230.

Mason, E. G.; South, D. B. and Zhao, W. 1996b. Performance of *Pinus radiata* in relation to seedling grade, weed control and soil cultivation in the central North Island of New Zealand. New Zealand J. For. Sci. 26(1/2): 173-183.

Mason, E. G. and Whyte, A. D. G. 1997. Modelling initial survival and growth of radiata pine in New Zealand. Acta Forestalia Fennica 255. pp. 38.

Mason, E. G., Whyte, A. G. D., Woollons, R. C. and Richardson, B. 1997. A model of the growth of juvenile radiata pine in the Central North Island of New

Zealand: links with older models and rotation-length analyses of the effects of site preparation. For. Ecol. Manage. 97: 187-195.

Mason, E. G. and Kirongo, B. B. 1999. Responses of radiata pine clones to varying levels of pasture competition in a semiarid environment. Can. J. For. Res. 29: 934-939.

Mason, E. G. and Milne, P. G. 1999. Effects of weed control, fertilization and soil cultivation on growth of *Pinus radiata* at mid-rotation in Canterbury, New Zealand. Can. J. For. Res. 29: 985-992.

Mason, E. G. (in prep.). An initial growth model that includes seedling quality, initial root collar diameter and handling practices.

Matthews, L. J. 1956. Chemical methods of weed control. New Zealand Department of Agriculture. Bulletin No. 329. Wellington. p. 63, 80.

McElwee, M., Irvine, J. I. and Burge, M. N. 1990. A mycoherbicidal approach to bracken control. IN: Basset, C.; Whitehouse, L. J. and Zabkiewicz (Eds.). "Alternatives to chemical control of weeds. Proccedings of an International conference. Rotorua, New Zealand, July 1989. Ministry of Forests. FRI Bulletin No. 155. p. 74-79.

McFadyen, E. C. Rachel 1998. Biological control of weeds. Annu. Rev. Entomol. 43: 369-93.

Mead, D. J. 1990. Response of young *Pinus radiata* to cultivation and fertilization near Motueka, New Zealand. New Zealand For. Sci. 20(3): 268-78.

Mead, D. J., Draper, D. and Madgwick, H. A. I. 1984. Dry matter production of a young stand of *Pinus radiata*: some effects of nitrogen fertiliser and thinning. NZ. J. For. Sci. 14(1): 97-108.

Mead, D. J., Lucas, R. J. and Mason, E. G. 1993. Studying interactions between pastures and *Pinus radiata* in Canterbury's subhumid temperate environment - the first 2 years. New Zealand Forestry. 38(1): 26-31.

Menzies, M. I. 1988. Seedling quality and seedling specifications of radiata pine. What's New in Forest Research No. 171. FRI, Rotorua, New Zealand.

Menzies, M. I. and Chavasse, C. G. R. 1982. Establishment trials on frost-prone sites. New Zealand Journal of Forestry. 27(1): 33 - 49.

Menzies, M. I., Chavasse, C. G. R., Bowles, G. P. and Balneaves, J. M. 1981. Nursery stock quality and establishment techniques for frost sites. IN: Forest

nursery and establishment practices. FRI symposium No. 22, 23rd- 27th March 1981, part II - establishment practices, Chavasse C. G. R. (eds.). New Zealand FRI. p. 154-165.

Menzies, M. I., Klomp, B. K., and Holden, D. G. 1991. Optimal physiological age of propagules for use in Clonal forestry. IN: Proceedings FRI/NZFP Forests Ltd, Clonal forestry Workshop 1-2 May 1989, Miller, J. T. (ed.). Rotorua New Zealand. FRI Bulletin No. 160. p. 142-146.

Mohren, G. M. J., Rabbinge, R. 1990. Growth-influencing factors in dynamic models of forest growth. IN: Process modeling of forest growth responses to environmental stress Dixon, R. K., Meldahl, R. S., Ruark, G. A. and Warren, W. G. (Eds.). Timber Press, Oregon, USA. p.229-240.

Morris, D. M. and Forslund, R. R. 1991. Field-oriented competition index for young jack pine plantations and a computerised decision tool for vegetation management. New For. 5(2): 93-107.

Mullin, T. J. and Bertrand, S. 1998. Environmental release of transgenic trees in Canada- potential benefits and assessment of biosafety. Forest Chronicle 74: 203-219.

Munson, A. D. and Timmer, U. R. 1990. Site specific growth and nutrition of planted *Picea mariana* in Ontario Caly Belt. III. Biomass and nutrient allocation. Can. J. For. Res. 20: 1165-1171.

Nambiar, E. K. S. and Zed, P. G. 1980. Influence of weeds on the water potential, nutrient content and growth of young radiata pine. Austr. For. Res. (10): 279-88.

Nambiar, E. K. S., and Sands, R. 1993. Competion for water and nutrients in forests. Can. J. For. Res. 23:1955-68.

New Zealand Forest owners Association (N.Z.F.O.A.) 1999. Facts and figures. New Zealand Forest industry. pp. 22.

New Zealand Official Year Book (N.Z.O.Y.B.) 1998. Statistics New Zealand, 101st Edition. G.P. publication. p. 413-420.

Newton, P. F. and Jolliffe, P. A. 1993. Above ground dry matter partitioning, size variation and competitive processes within second growth Black spruce stands. Can J. For. Res. 23:1917-1929.

Ngugi, M. R. 1996. Growth and yield models for *Cupressus lusitanica* (Mill.) and *Pinus putula* (Schect & Cham.) grown in Kenya. Msc. Thesis. University of Canterbury (Christchurch), New Zealand .

Nilsson, U. and Albrektson, A. 1993. Productivity of needles and allocation of growth in young Scots pine trees of different competitive status. Forest Ecology and Management. 62: 173-187.

Nugroho, B. A. P. 1999. Soil CO_2 and O_2 concentrations under radiata pine in competition with pasture or weeds: Impacts on root growth and respiration. MSc. Thesis, University of Canterbury (Christchurch).

Olsen, P. 1997. Breeding trait gains and economic worth. . IN: Proceedings of IUFRO '97: Genetics of radiata pine, 1-4 December 1997, Rotorua, New Zealand. FRI Bulletin No. 203. p. 8.

Parham, B. E. V. and Healy, A. J. 1976. Common weeds in New Zealand: An illustrated guide to their identification. A. R. Shearer. Government Printer. Wellington, New Zealand. pp.173.

Payandeh, B. 1987. PLANT: A model for artificial forest regeneration in Ontario. IN: Forest Growth Modelling and Prediction, volume 1. Proceedings of an UIFRO symposium August 23rd - 27th 1987, Minneapolis, Minnesota, USA. Society of American Foresters Publication Number SAF-87.12. p. 386-393.

Perkins, T. D. and Adams, G. T. 1995. Rapid freezing induces winter symptomatology in red spruce foliage. Tree Physiology. 15: 259-266.

Perry, M. A., Mitchell, R. J., Zutter, B. R., Glover, G. R. and Gjerstad, D. H. 1993. Competition responses of Loblolly pine to gradients in Loblolly pine, sweet gum and broom sedge densities. Can. J. For. Res. 23: 2049-2058.

Pienaar, L. V. and Rheney, J. W. 1995. Modelling stand level growth and yield responses to silvicultural treatments. For. Sci. 41: 629-638.

Pitt, D. G. and Glover, G. R. 1993. Large-scale 35 mm aerial photos for assessment of vegetation management research plots in eastern Canada. Can. J. For. Res. 23: 2159-2169.

Pitt, D. G. and Glover, G. R. 1996. Measurements of woody plant attributes from large-scale aerial photographs. N.Z. J. For. Sci. 26(1/2): 53-73.

Pitt, D. G., Dumas, M. T., Wall, R. E., Thompsom, D. G., Lanteigne, L., Hintz, W., Sampson, G. and Wagner, R. G. 1999. *Chondrostereum purpureum* as a

biological control agent in forest vegetation management. I. Efficacy on speckled alder, red maple and aspen in eastern Canada. Can J. For. Res. 29:841-851.

Pook, E. W. 1984. Canopy dynamics of *Eucalyptus maculata* Hook II: Canopy Leaf area balance. Austr. J. Bot. 32: 405 - 413.

Powers, R. F. and Reynolds, P. E. 1999. Ten-year responses of Ponderosa pine plantations to repeated vegetation and nutrient control and environmental gradient. Can. J. For. Res. 29: 1027-1038.

Preest, D. S. 1985. Chemical aids to planting site preparation. N.Z. FRI Bulletin. No. 100.

Purey-Cust, J. and Hammond, D. R. 1995. A condensed history of Forestry in New Zealand. Forestry Handbook - Don Hammond (ed.). New Zealand Institute of Foresters (Inc.) p. 26-29.

Radcliffe, J. E. 1990. Gorse control by goats: effective strategies in Canterbury. IN: Basset, C.; Whitehouse, L. J. and Zabkiewicz (Eds.). "Alternatives to chemical control of weeds. Proccedings of an International conference. Rotorua, New Zealand, July 1989. Ministry of Forests. FRI Bulletin No. 155. p. 144-149.

Radosevich, S. R. and Oysteryoung, K. 1987. Principles governing plant-environment interactions. IN: Forest Vegetation Management for conifer production. Walstad, J. D. and Kuch, J. P. (eds.). John Wiley and sons. p. 105-156.

Radosevich, S. R., Wagner, R. G. and Roush, M. C. 1990. Weed competition and control options in US forestry. IN: Basset, C.; Whitehouse, L. J. and Zabkiewicz (Eds.). "Alternatives to chemical control of weeds. Proccedings of an International conference. Rotorua, New Zealand, July 1989. Ministry of Forests. FRI Bulletin No. 155. p. 103-110.

Raison, R. J., Khanna, P. K., Benson, M. L., Myers, B. J. and McMurtrie, R. E. 1992a. Dynamics of *Pinus radiata* foliage in relation to water stress and nitrogen stress: II. Needle loss and temporal changes in total foliage mass. Forest Ecology and Management. 52: 159 - 178.

Raison, R. J., Myers, B. J. and Benson, M. L. 1992b. Dynamics of *Pinus radiata* foliage in relation to water stress and nitrogen stress: I. Needle production and properties. Forest Ecology and Management. 52: 139 - 158.

Ray, J. W. 1981. Nursery diseases. IN: Forest nursery and establishment practices. FRI symposium No. 22, 23rd- 27th March 1981, Chavasse C. G. R. (eds.). New Zealand FRI. p. 74-78.

Ray, J. W. and Richardson, B. 1993. A rapid screening method for selecting grass species with potential for suppressing pampas growth. Proceedings of the 46th New Zealand plant protection conference. New Zealand plant protection Society Inc. 1993. p. 313-318.

Richardson, B. 1993. Vegetation management practices in plantation forests of Australia and New Zealand. Can. J. For. Res. 23: 1989-2005.

Richardson, B., Vanner, A., Davenhill, N. Balneaves, J., Miller, K. and Ray, J. 1993. Interspecific competition between *Pinus radiata* and some common weed species - first-year results. New Zealand J. For. Sci. 23: 179-193.

Richardson, B., Davenhill, N., Coker, G., Ray, J., Vanner, A. and Kimberly, M. 1996a. Optimising spot weed control: First approximation of the most cost-effective spot size. New Zealand J. For. Sci. 26(1/2) 265-275.

Richardson, B., Vanner, A., Ray, J., Davenhill, N. and Coker, G. 1996b. Mechanisms of *Pinus radiata* growth suppression by some common weed species. New Zealand J. For. Sci. 26: 421-437.

Richardson, B., Kimberley, M. O., Ray, W. J. and Coker, G. W 1999. Indices of interspecific plant competition for *pinus radiata* in the central north island of New Zealand. Can. J. For. Res. 29: 898-905.

Rook, D. A. and Menzies, M. I. 1981. Methods of determining physiological quality of planting stock. IN: Forest nursery and establishment practices. FRI symposium No. 22, 23rd- 27th March 1981, Chavasse C. G. R. (eds.). New Zealand FRI. p. 159-169.

Rook, D. A., Bollmann, M. P. and Hong, S. O. 1987. Foliage development within the crowns of *Pinus radiata* trees at two spacings. New Zealand J. For. Sci. 17(2/3): 297-314.

Rook, D.A. and Whyte, A. G. D. 1976. Partial defoliation and growth of five-year-old radiata pine. NZ. J. For. Sci. 6(1): 40-56.

Roy, B., Popay, I., Champion, P., James, T. and Rahman, A. 1998. An Illustrated Guide to common weeds of New Zealand. Published by New Zealand plant protection society (inc.). New Zealand.

Sands, R. and Nambiar, E. K. S. 1984. Water relations of *Pinus radiata* in competition with weeds. Can. J. For. Res. 14: 233-237.

Sands, R., Nugroho, B. P., Leung, D. W. M., Sun, O. J., and Clinton, W. P. 2000. Changes in soil CO_2 and O_2 concentrations when radiata pine is grown in competition with pasture or weeds and possible feedbacks with radiata pine root growth and respiration. Plant and Soil. (in press).

SAS Institute Inc. 1996. SAS/STAT™ 6.12. Guide for personal computers, version 6 Edition. Cary NC. SAS Institute.

Senyk, J. P. and Smith, R. B. 1991. Estimating impacts of forest harvesting and mechanical site preparation practices on productivity in British Columbia. IN: Long-term field trials to assess environmental impacts of harvesting. Dyck, W. J. and Mees, C. A. (Eds.). Proceedings of IEA/BE T6/A6 workshop, Florida, U. S. A. Report No. 5. N.Z. F.R.I. Bulletin No. 161. p. 199-211.

Shakespeare, W. The tragedy of King Richard II, Act III, scene IV. MaCMillan and Company limited (1950).

Shelbourne C. J. A. 1986. Role of genetic improvement. Forestry Handbook - Levack, H. (eds.). New Zealand Institute of foresters (Inc.) p. 44-45.

Shelbourne, C. J. A. 1991. Clonal testing *Pinus radiata* in New Zealand. IN: Proceedings FRI/NZFP Forests Ltd, Clonal forestry Workshop 1-2 May 1989, Miller, J. T. (ed.). Rotorua, New Zealand. FRI Bulletin No. 160. p. 25-40.

Shelbourne, C. J. A. 1997. Genetics of adding value to the end-products of radiata pine. IN: Proceedings of IUFRO '97: Genetics of radiata pine, 1-4 December 1997, Rotorua, New Zealand. Burdon, R. D. and Moore, J. M. (eds.). FRI Bulletin No. 203. p. 129-141.

Shelbourne, C. J. A., Apioloza, L. A., Jayawickrama, K. J. S. and Sorensson, C. T. 1997. Developing Breeding objectives for radiata pine in New Zealand. IN: Proceedings of IUFRO '97: Genetics of radiata pine, 1-4 December 1997, Rotorua, New Zealand. Burdon, R. D. and Moore, J. M. (eds.). FRI Bulletin No. 203. p. 160-168.

Shelton, M. G. and Switzer, G. L. 1984. Variation in the specific leaf area relationships of Loblolly pine fascicles. For. Sci. 30: 355-363.

Skinner, M. F., Murphy, G., Robertson, E. D. and Firth, J. G. 1989. Deleterious effects of soil disturbance on soil properties and subsequent early growth and second rotation radiata pine. IN: W. C. Dyck and C. A. Mees (eds.). Research strategies for long-term site productivity. IEA/BE A3 Report No. 8. Forest Research Institute, New Zealand, Bulletin 152. p. 201-212.

Smethurst, P. J. and Nambiar, E. K. S. 1989. Role of weeds in the management of nitrogen in a young *Pinus radiata* plantantion. New For. 3: 203-224.

Snowdon, P. 1985. Effects of fertilization and family on the homogeneity of biomass regressions for young *Pinus radiata*. Aust. For. Res. 15: 135-140.

Snowdon, P. and Benson, M. L. 1992. Effects of combinations of Irrigation and fertilization on the growth and above-ground biomass production of *Pinus radiata*. For. Ecol. and Mgt. 52(1-4): 87-116.

Snowdon, P. and Waring, H. D. 1984. Long-term nature of growth responses obtained to fertilizer and weed control applied at planting and their consequences for forest management. IN: Proceedings of the IUFRO symposium on site and site productivity of fast growing plantations. Vol. 2. Grey, D. C. and Schonau, A. P. G. (Eds.). South African FRI, Pretoria. South Africa.

Snowdon, P. and Khana, P. K. 1989. Nature of growth responses in long-term field experiments with special references to *Pinus radiata*. IN: W. C. Dyck and C. A. Mees (eds.). Research strategies for long-term site productivity. IEA/BE A3 Report No. 8. Forest Research Institute, New Zealand, Bulletin 152. p. 173 - 186.

Snowdon, P. and Waring, H. D. 1985. Responses of genotypes of *Pinus radiata* to clover and fertilization. Aust. For. Res. 15: 125-134.

South, D. B. 1991. Testing the hypothesis that mean relative growth rate eliminates size related growth differences in tree seedlings. New Zealand J. For. Sci. 21(2/3): 144-164.

South, D. B. 1995. Relative growth rates: A critique. South African For. J. 173: 43-48.

Squire, R. O. 1977. Interacting effects of grass competition, fertilizing and cultivation on the early growth of *Pinus radiata* D. Don. Austr. For. Res. Vol. 7(4): 247-252.

Stearn, W. T. 1956. A review of "weeds" by W. C. L. Muenscher (Macmillan, New York 1984). J. of the Royal Horticultural Society. 81: 285-6.

Sutherland, O. W. R. and Hill, R. L. 1990. History and protocols for biological control of weeds in New Zealand. Basset, C.; Whitehouse, L. J. and Zabkiewicz (Eds.). "Alternatives to chemical control of weeds. Proccedings of an International conference. Rotorua, New Zealand, July 1989. Ministry of Forests. FRI Bulletin No. 155. p. 18-24.

Sutton, W. R. J. 1981. The importance of fully effective establishment in relation to subsequent tending operations and to crop quality and value. IN: Forest nursery and establishment practices. FRI symposium No. 22, 23rd- 27th March 1981, part II - establishment practices, Chavasse C. G. R. (eds.). New Zealand FRI. p. 35-36.

Sutton, W. R. J. 1991. Implications of establishment practice. IN: Proceedings of an IUFRO symposium, 11-15th September 1989. Menzies, M. I.; Parrott, G. E. and Whitehouse, L. J. (eds.). New Zealand Ministry of Forestry, FRI Bulletin No. 156. p. 13-15.

Sweet, G. B. and Wareing, P. F. 1966. The relative growth rates of large and small seedlings in forest tree species. Forestry supplement: 110-117.

Tappeiner II., J. C. and Wagner, R. G. 1987. Principles of silvicultural prescriptions for vegetation management. IN: Forest Vegetation Management for conifer production. Walstad, J. D. and Kuch, J. P. (eds.). John Wiley and sons. p. 399-429.

Taylor, J. A. 1990. Towards an integrated bracken control technology. IN: Basset, C.; Whitehouse, L. J. and Zabkiewicz (Eds.). "Alternatives to chemical control of weeds. Proccedings of an International conference. Rotorua, New Zealand, July 1989. Ministry of Forests. FRI Bulletin No. 155. p. 40-46.

Temu, M. J. 1992. Forecasting yield of Douglas fir in the South Island of New Zealand. Ph.D. Thesis, University of Canterbury (Christchurch), New Zealand.

Ter-mikaelian, T. M., Wagner, R. G., Bell, F. W. and Shropshire, C. 1999. Comparison of Photosynethtically Active Radiation and cover estimation for measuring the effects of inter-specific competition on jack pine seedlings. Can. J. For. Res. 29: 883-889.

The Concise Oxford Dictionary 1995. 9th Edition, edited by Della Thompson. Clarendon Press. Oxford. p. 248.

Theodorou, C., Cameron, J. N., and Bowen, G. D. 1991. Root characteristics of several *Pinus radiata* Genotypes growing on different sites in Gippsland. Austr. For. 54 (1&2): 40-51.

Tombleson, J. D. and Carson, M. J. 1991. Family forestry vs clonal forestry: a case study. IN: Proceedings FRI/NZFP Forests Ltd, Clonal forestry Workshop 1-2 May 1989, Miller, J. T. (ed.). Rotorua New Zealand. FRI Bulletin No. 160. p. 150-154.

Trewin, A. R. D. 1981. The importance of a good outplanting system for the establishment of bare-root pine seedlings. IN: Forest nursery and establishment practices. FRI symposium No. 22, 23rd- 27th March 1981, part II - establishment practices, Chavasse C. G. R. (eds.). New Zealand FRI. p. 226-244.

Trewin, A. R. D. and Cullen, A. W. J. 1985. A fully integrated system for planting bare-root seedlings of radiata pine in New Zealand. IN: Proceedings of an IUFRO symposium on "Nursery management practices for southern pines". Montgomery, Alabama, USA.

Universal Imaging Corporation 1995. Metamorph Imaging System, Summary guide. Image-1/Metamorph Imaging System. Version 2 for MS windows. Universal Imaging Corporation. USA.

Van den Driessche, P. and Van den Driessche, R. 1991. Growth analysis. IN: Van den Driessche, R. (eds.). Mineral nutrition of Conifer seedlings. CRC press, Boca Raton, Florida.

Van den Driessche, R. 1992. Absolute and relative growth of D. fir seedlings of different sizes. Tree physiology 10: 141-52.

Van Dorsser, J. C. 1981a. Nursery weed control. IN: Forest nursery and establishment practices. FRI symposium No. 22, 23rd- 27th March 1981, Chavasse C. G. R. (eds.). New Zealand FRI. p. 84-101.

Van Dorsser, J. C. 1981b. Seedling conditioning. IN: Forest nursery and establishment practices. FRI symposium No. 22, 23rd- 27th March 1981, Chavasse C. G. R. (eds.). New Zealand FRI. p. 128-142.

Van Rossen, R. and West, G. G. 1993. Cut-over sowing for weed control and improved tree growth. IN: Proceedings of weed works' 93 workshop on "Forest weed control".

Vanclay, J. K. 1994. Modelling forest growth and yield: Application to mixed Tropical forests. CAB International.

Viles, D. G. K. 1981. To plant or not to plant. IN: Forest nursery and establishment practices. FRI symposium No. 22, 23rd- 27th March 1981, part II - establishment practices, Chavasse C. G. R. (eds.). New Zealand FRI. p. 1-11.

Wagner, R.G. Peterson, T.D., Ross, T.W., and Radosevich, S.R., 1989, Competition thresholds for the survival and growth of Ponderosa pine seedlings associated with woody and herbaceous vegetation, New Forests 3 (2): 151-170.

Wagner, R. G., Radosevich, S. R. 1991a. Neighbourhood predictors of interspecific competition in young Douglas-fir plantations. Can. J. For. Res. 21: 821-828.

Wagner, R. G., Radosevich, S. R. 1991b. Interspecific competition and other factors influencing the performance of D. fir in the Oregon coast range. Can. J. For. Res. 21: 829-835.

Wagner, R. G. 1993. Research directions to advance forest vegetation management in North America. Can. J. For. Res. 23: 2317-2327.

Wagner, R. G. and Radosevich, S. R. 1998. Neighbourhood approach for quantifying interspecific commpetition in coastal Oregon forests. Ecological Applications No. 8: 779-794.

Wagner, R. G., Mohamed, G. H. and Noland, T. L. 1999. Critical period of interspecific competition for northern conifers associated with herbaceous vegetation. Can. J. For. Res. 29: 890-897.

Walstad, J. D. and Kuch, P. J. 1987. Introduction to forest vegetation management. IN: Forest Vegetation Management for conifer production. Walstad, J. D. and Kuch, J. P. (eds.). John Wiley and sons. p. 3-14.

Walstad, J. D., Newton, M. and Gjerstad, D. H. 1987. Overview of vegetation management alternatives. IN: Forest Vegetation Management for conifer production. Walstad, J. D. and Kuch, J. P. (eds.). John Wiley and sons. p.157-200.

Walter, C., Carson, M., Charity, J., Donaldson, S., Gardner, R., Gemmell, J., Grace, L., Holland, L., McFetridge, P., Menzies, M., Wagner, A. and Walden, A.

1997. Transformation and gene expression in *Pinus radiata*. IN: Proceedings of IUFRO '97: Genetics of radiata pine, 1-4 December 1997, Rotorua, New Zealand. FRI Bulletin No. 203. p. 319-332.

Wang, Y. P. and Jarvis, P. G. 1990. Influence of crown structural properties on PAR absorption, photosynthesis and transpiration in Sitka spruce: application of a model (MAESTRO). Tree Physiology. 7: 297-316.

Wareing, P. F. 1966. The physiologist's approach to tree growth. Forestry supplement: 7-18.

Waring, R. H. and Running, S. W. 1998. Forest Ecosystems: Analysis at multiple scales. 2nd Edition. Academic Press. pp 365.

Watts, W. R., Neilson, R. E. and Jarvis, P. G. 1976. Photosynthesis in Sitka spruce (*Picea sitchenisis* (BONG.) CARR.): VII Measurements of stomatal conductance and $^{14}CO_2$ uptake in a forest canopy. J. Appl. Ecol. (13): 623 - 638.

Webb, M. and Conroy, C. 1995. The socio-economics of weed control on small-holder farms in Uganda. Proc. Brighton Crop Prot. Conf.-Weeds. 1: 157-162.

Weisberg, S. 1985. Applied linear regression. 2nd Edition. John Wiley and Sons.

West, C. Briggs, G. E. and Kidd, F. 1920. Methods and significant relations in the quantitative analysis of plant growth. New Phytologist. 19: 200-207.

West, G. G. 1981. The effects of grass competition and fertilizer on the initial height growth of radiata pine seedlings and cuttings at four sites. IN: Forest nursery and establishment practices. FRI symposium No. 22, 23rd- 27th March 1981, part II - establishment practices, Chavasse C. G. R. (eds.). New Zealand FRI. p. 126-130.

West, G. G. 1984. Establishment requirements of *Pinus radiata* cuttings and seedlings compared. New Zealand J. For. Sci. 14(1):41-52.

West, G. G. and Dean, M. G. 1990. The use of livestock to control weeds in New Zealand forests. IN: Basset, C., Whitehouse, L. J., Zabkiewicz, J. (eds.). "Alternatives to the chemical control of weeds". Proceedings of an International conference, Rotorua, New Zealand, July 1989. Ministry of Forests. FRI Bulletin 155. pp. 128-132.

West, G. G. and Dean, M. G. 1992. Oversowing: the race to occupy forest sites. Whats' New in Forest research. No. 223. NZ FRI Rotorua.

West, G. G., Knowles, R. L. and Koehler, A. R. 1982. Model to predict the effects of pruning and early thinning on the growth of Radiata pine. NZ. For. Serv. FRI Bulletin No. 5.

Westoby, J. 1987. The purpose of Forests: Follies of Development. Balckwell Ltd. p. 3-70.

Whyte, A. D. G. 1994. Modelling growth and yield of tropical plantations. An IUFRO Symposium on growth and yield of Tropical Forests. September 26 - October 1 1994. Kenohiro, Y. (compiler). Tokyo, Japan.

Will, G. 1985. Nutrient deficiencies and fertilizer use in New Zealand exotic forests. FRI Bulletin No. 97.

Willoughby, I. 1999. Future alternatives to the use of herbicides in British forestry. Can. J. For. Res. 29: 866-874.

Woodman, J. N. 1971. Variation of net photosynthesis within the crown of a large forest grown conifer. Photosynthetica. 5(1): 50 - 54 (Abstracts).

Woollons, R. C. 1998. Even-aged stand mortality estimation through a two-step regression process. Forest Ecology and Management 105: 189-195.

Woollons, R. C., Whyte, A. G. D. and Mead, D. J. 1988. Long-term growth responses in *Pinus radiata* fertilization experiments. N.Z. J. For. Sci. 18: 199-209.

Woolons, R.C., Snowdon, P. and Mitchell, N. D., 1998. Augmentating Empirical stand projection equations with edaphic and climatic variables. For. Ecol. Manage. 98(3): 267-275.

Xu, H. 2000. Modelling Photosynthetic CO_2 fixation among radiata pine clones with contrasting crown characteristics at age 5 at Dalethorpe, Canterbury. Ph.D. thesis, University of Canterbury (Christchurch).

Zabkiewicz, J. A. and Richardson, B. 1990. Weed control in New Zealand forests-costs, contraints and future options. IN: Basset, C.; Whitehouse, L. J. and Zabkiewicz (Eds.). "Alternatives to chemical control of weeds. Proccedings of an International conference. Rotorua, New Zealand, July 1989. Ministry of Forests. FRI Bulletin No. 155. p. 111-115.

Zedaker, S. M., Smith, D. W., Seiler, J. R. and Kreh, R. E. 1993. Interference interactions in experimental pine-hardwood stands. Can. J. For. Res. 23: 2032-2043.

Zhao, W. 1999. Growth and yield Modelling of *Pinus radiata* in Canterbury, New Zealand. Ph.D thesis, University of Canterbury (Christchurch).

Zou, C., Sands, R. and Sun, O. 2000. Physiological responses of radiata pine roots to soil strength and soil water deficit. Tree Physiology. 20: 1-3.

Zutter, R. B., Gjerstad, H. D. and Glover, R. G. 1986. Effects of interfering vegetation on biomass, fascicle morphology and leaf area of Loblolly pine seedlings. For. Sci. 32: 1016 - 1031.

Zutter, B. R., Miller, J. H., Allen, H. L. Zedaker, S. M., Edwards, M. B. and Newbold, R. A. 1999a. Fascicle nutrient and biomass responses of young loblolly pine to control of woody and herbaceous competitors. Can. J. For. Res. 29: 917-925.

Zutter, B. R., Mitchell, R. J., Glover, G. R. and Gjerstad, G. H. 1999b. Root length and biomass in mixtures of broom sedge with loblolly pine or sweet gum. Can. J. For. Res. 29: 926-933.

APPENDICES

APPENDIX 1

Rainfall and temperature data of the closest weather station to the experiment.

APPENDIX 2

A reprint of the summary of a paper presented at the "Third International Conference on Forest Vegetation management: popular summaries" (24th - 28th August 1998). Forest Research Information paper No. 121. Ontario FRI, Canada.

APPENDIX 3

Abstract of a paper presented at "The 6th National New Zealand Postgraduate Conference on Strength in Diversity" (19th - 21st November 1999). University of Canterbury, Christchurch, New Zealand.

APPENDIX 4

Reprint of a paper published in the Canadian Journal of Forest Research in 1999. The paper is titled " Responses of radiata pine clones to varying levels of pasture competition in a semiarid environment.

APPENDIX 5

A letter from the Co-Editor-in-Chief of the Journal of Ecology and Management regarding a manuscript submitted to their journal. The Manuscript is titled "Interference mechanisms of pasture on the growth and fascicle dynamics of 3-year old radiata clones".

APPENDIX 1

Rainfall and temperature data for Hororata which was the closest weather station to the exprimental site (Source: New Zealand climate digest, National Institute of Water and Atmospheric Research (NIWA) Ltd.)

Month and year	Rainfall (mm)		Temperatures in degrees centigrade (°C)		
	Total	No. of days	Maximum	Minimum	Average
Sept. 1996	12	7	17.7	5.3	11.5
Dec. 1996	84	10	-	-	-
March 1997					
May 1997	66	11	15.1	2.6	8.9
Sept. 1997	53	12	13.0	1.9	7.5
Dec. 1997	46	11	21.0	6.9	14.0
March 1998	65	9	22.7	9.4	16.1
May 1998	60	8	16.0	3.7	9.9
Sept. 1998	23	10	15.9	2.1	9.0
Dec. 1998	17	5	22.6	7.9	15.3
March 1999	89	10	22.5	9.6	16.1
May 1999	17	6	17.0	2.9	10.0

The months shown in the table were those in which some measurements were taken at the experiment.

USING IMAGE ANALYSIS AND CANOPY MEASUREMENTS TO CHARACTERISE THE GROWTH AND MORPHOLOGY OF JUVENILE RADIATA PINE (*Pinus radiata* D. Don) CLONES SUBJECTED TO DIFFERENT WEED COMPETITION LEVELS.

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Introduction

Carbon fixation in trees has been related to the amount, temporal and spatial distribution of foliage and light interception (Kinerson *et al.* 1974, Grace *et al.* 1987, and Hunter *et al.* 1987). Biotic (diseases, pests, competition) and abiotic (temperature, rainfall, fungi) agents (Kinerson *et al.* 1974) and the genetic make-up also play a crucial role in determining growth. Tree crowns are therefore, vital as they are the sites where most physiological processes important for growth, for example light interception, photosynthesis and respiration take place (Beets and Lane 1987).

Competition affects the morphology and physiology of subject trees (Nambiar and Zed 1980, Zutter *et al.* 1986, Beets and Lane 1987), but only a few researchers have endeavoured to characterise competition effects using tree morphological characteristics, for example crown density and structure. Many studies on interspecific competition effects in juvenile plantations still continue to use only diameter and height and/or their derivations to measure competition effects. Perhaps as Landsberg (1986) correctly observes, the time and cost and destructive methods involved in collecting physiological data make the approach less feasible. Understanding how different clones may react physiologically and morphologically to stress effects may lead to improved models of competition, and ultimately better weed control strategies.

The purpose of this paper therefore is to explore the use of simple morphological measures for quantifying interspecific competition effects and to discuss the relationships between these measures to the more commonly used variables; height and diameter.

Materials and Methods

Data for this study came from an on-going 1.5-year-old genotype-by-competition experiment. A randomised complete block design with 3 replications was used. Weeding treatments formed the main plots while clones were the sub-plots. The weeding treatments used were: 1) no competition (i.e. complete weeding); 2) 3.14 m^2 weed-free spots around individual radiata plants; 3) 0.75 m^2 spots; and 4) the control, 0.03 m^2 spots only at planting. Mason and Kirongo (1998 - in this conference) give a detailed discourse on the experimental design and lay out, as well as an analysis of stem measurements.

Detailed morphological studies were carried out on three of seven clones designated Cl1, Cl2 and Cl3. These represented the poorest, medium and fastest growing clones. All trees were assessed for total height and ground line diameter (GLD). Four trees spanning a range of sizes were

Wagner, R.G. and D.G. Thompson (comp.). 1998. Third International Conference on Forest Vegetation Management: Popular summaries. Ont. Min. Nat. Resour., Ont. For. Res. Inst., For. Res. Info. Pap. No. 141.

chosen from each of the 3 clones in all the treatments (144 trees). The total number of whorls and their height above ground were measured. Length of all branches, branch order, and branch diameter at the point of inception were also recorded. Permanent sample plots were marked using out door water-based paint on two representative branches on each branch whorl. The plots were allocated so as to account for vertical height, crown depth, branch order and needle age effects. Fascicle numbers and average needle lengths were assessed every 4-8 weeks. The primary aim was to enable reliable estimates of needle losses and hence crown foliage growth dynamics especially during the main summer growing season.

Photographs of 289 tree crowns were taken using a digital camera. Crown photo areas were calculated using Metamorph image analysis package (Universal Image Analysis 1995). Data were analysed using SAS statistical package (SAS/STATS 6.12, SAS Inst. Inc. 1996). The results reported here do not include crown foliage growth dynamics as only one season's measurements have been collected. Leaf area measures and biomass estimates from some destructively sampled trees are also excluded for the same reason.

Results and Discussion

Mean height and GLD growth results at age 1.5 years are similar to those reported by Mason and Kirongo (1998 - in this conference). Significant differences in both height ($P<0.0002$) and GLD ($P<0.0001$) mean growth between competition levels and clonal effects ($P<0.0080$ for height and $P<0.0010$ for GLD) were observed.

Weeding influenced above ground productivity immensely. Crown structure expressed using mean branch number ($P<0.0372$) and branch length ($P<0.0002$) was highly significant between weeding treatments. Branch length was not significantly different between clones, but branch numbers were highly significant ($P<0.0002$). Meanwhile crown density as expressed using crown photo areas was highly significant between competition ($P<0.0098$) as well as clones ($P<0.0001$) (Figure 1). Percent mean branch numbers ranged from 35.5% to 50.5% while branch length differences ranged from 48.1% to 66.5% between the control (Wc0.03) and the weeded treatments. Clones showed significant differences in branch number and length (Figure 2). Percent differences of between 18.3% to 38.6% for branch numbers and 12% to 32% for branch lengths were observed at age 1.5 years. Mean number of whorls per tree ranged from 2.83 to 4.76 for weeding and 3.20 to 4.58 for clones.

Figure1. Crown photo area by increasing competition

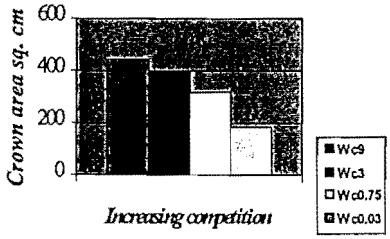
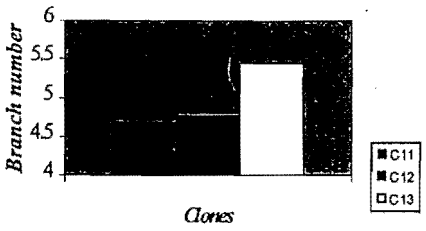


Figure 2. Mean branch number by clones.



Clonal effects were more pronounced when comparisons were based on above ground productivity. Many studies have reported strong genotype-by-environment interaction (e.g. Landsberg 1986, Theodorou *et al.* 1991, and Madgwick 1994). In this study, trees in the control (Wc0.03) looked chlorotic with very short branches and tiny needles. In contrast trees in the weeded treatments were green with needles which were long and healthy looking. Mean needle length in the unweeded treatments was between 40-60 mm. In contrast, needle lengths in the weeded treatments ranged from 90 to 120 mm, a two-fold difference. Nambiar and Zed (1980) and Zutter *et al.* (1986) reported similar findings. Needle lengths were not significantly different between clones. It is possible that different clones may start and end growth at different times in the season and this will be investigated in the coming growth season.

These results reaffirm that competition from weeds affects tree morphology, probably physiology, and ultimately growth. The observation that stressed trees produced fewer branches may be due to less primodia formation (Bollman *et al.* 1986). Rook *et al.* (1987) report clonal variation in branch numbers and our results concur. Different clones have different crown sizes (photo area) and this may be because different clones display different crown architecture, a hypothesis that will be tested in a future study. This could be important in minimising self-shading which can be a significant cause of light interception.

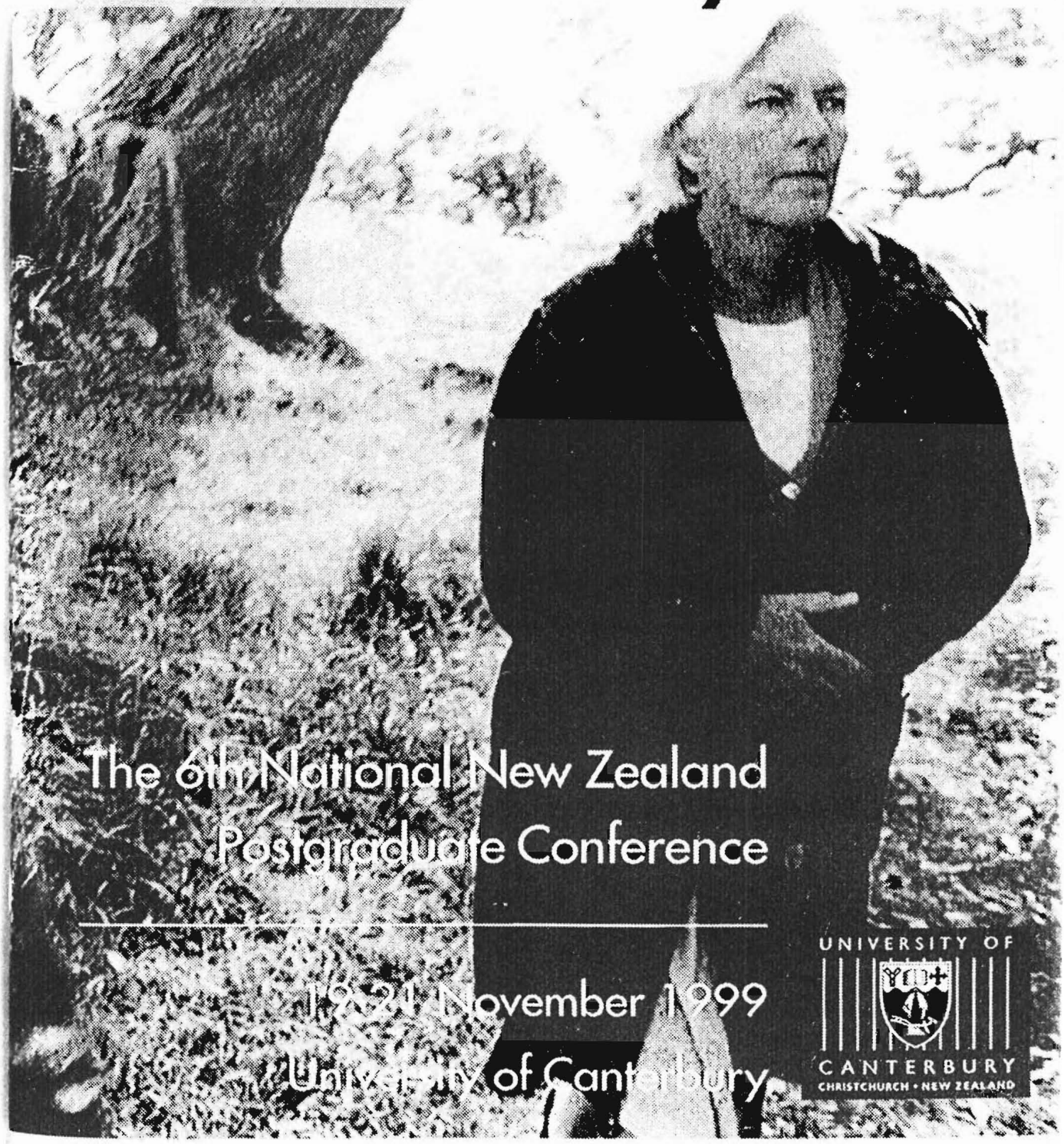
In this study, no significant genotype-by-site interactions were observed at age 1.5 years. However, mean branch number, length and crown density were observed to be sensitive to pasture competition gradients, like height and GLD growth variables. These variables are more closely related to morphological and physiological determinants of growth than are height and GLD. Observations of crown structure, leaf area and seasonal effects on foliage production are on going, and there appears to be potential to use crown measurements to explain growth. Sound relationships between crown measurements and leaf area and/or tree biomass, if well developed using limited destructive sampling and image analysis, could form a basis for less destructive methods of monitoring carbon fixation in young trees, and may shed light on why relative growth rate does not fit observed patterns of juvenile tree growth (Mason *et al.*1996).

References

Beets and Lane 1987. New Zealand J. For. Sci. 17(2/3): 283-91.
Bollman *et al.* 1986. Can. J. For. Res. 16: 1019-1029.
Grace J. C. *et al.* 1987. New Zealand J. For. Sci. 17(2/3): 193-209.
Hunter, I. R. *et al.* 1987. New Zealand J. For. Sci. 17(1): 67-75.
Kinerson *et al.* 1974. The dynamics of foliage distribution within a forest canopy.
Landsberg, J. J. 1986. Physiological Ecology of Forest Production. Academic press.
Madgwick, H. A. I. 1994. *Pinus radiata* - Biomass, Form and Growth. Rotorua, New Zealand.
Mason, E. *et al.* 1996. IUFRO conference, Denmark. p. 221-230.
Mason and Kirongo 1998. In this conference.
Nambiar, E. K. S. and Zed, P. G. 1980. Austr. For. Res. 10: 279-88.
Rook *et al.* 1987. New Zealand J. For. Sci. 17(2/3): 297-314.
SAS Institute Inc. 1996. SAS/STAT™ 6.12. Cary NC. SAS Institute.
Theodorou, C. *et al.* 1991. Austr. For. 54 (1&2): 40-51.
Universal Image Analysis 1995.
Zutter, R. B. *et al.* 1986. For. Sci. 32: 1016 - 1031.

Wagner, R.G. and D.G. Thompson (comp.). 1998. Third International Conference on Forest Vegetation Management: Popular summaries. Ont. Min. Nat. Resour., Ont. For. Res. Inst., For. Res. Info. Pap. No. 141.

strength in diversity



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Effects of Varying Competition on Crown Density, Needle Elongation and Specific Leaf Areas of 3 Radiata Pine Clones

Balozi Kirongo, School of Forestry, University of Canterbury

Crown areas, needle elongation and specific leaf areas of 3 juvenile radiata pine (Pinus radiata D Don.) clones growing under four pasture competition levels (total weeding, 2 m diameter spots, 1 m diameter spots and no weeding) were studied in a semi-arid environment in the Canterbury plains of the South Island, New Zealand.

Results at age 3 years showed that competition significantly influenced crown surface area ($P < 0.0003$), specific leaf area ($P < 0.0049$) and needle elongation ($P < 0.0001$). Trees growing without weeds initiated their needles earlier during the growing season and recorded highest needle elongation. Trees in weedy plots had higher specific leaf areas (SLA) compared to those in the other growing environments. There were significant differences in crown surface area ($Pr < 0.0135$) and needle elongation ($Pr < 0.0001$) among the clones. Specific leaf area did not differ significantly among the clones. No weeding by genotype interaction was evident for all the variables assessed.

In sites with water scarcity during the summer growing season like in the Canterbury plains, controlling pasture had 2 beneficial effects; 1) earlier needle initiation and therefore a longer growing season, and 2) ample leaf area development and growth.

Key words

Radiata pine, weed control, clones, crown area, needle elongation, specific leaf area.

Responses of radiata pine clones to varying levels of pasture competition in a semiarid environment

E.G. Mason and B. Kirongo

Abstract: An experiment comprising seven clones with four levels of weed competition was established on a semiarid site on the Canterbury plains, New Zealand, during September 1996. Previous experiments showed that trees subjected to little competition from weeds did not always respond to their favourable environments, resulting in more variation among individuals subjected to less competition. The aim of this experiment was to determine whether the variable response to competitive environment is partly a genetic effect. The main plots consisted of four levels of competition: no competition and cleared spots: 3.14, 0.75, and 0.03 m^2. Within each plot there were 10 individuals of each clone. Trees generally grew more rapidly with increasing amounts of clear ground, but increasing spots beyond 3.14 m^2 did not increase growth during the first year. Variation, expressed as coefficient of variation, was greater among trees subjected to more competition. Within clone coefficient of variation was not related to level of competition.

Résumé : Un dispositif expérimental comprenant sept clones et quatre niveaux de compétition par les mauvaises herbes a été établi sur un site semi-aride dans la plaine de Canterbury, en Nouvelle-Zélande, en septembre 1996. Des expériences précédentes montrent que les arbres soumis à une faible compétition par les mauvaises herbes ne réagissent pas toujours à cet environnement favorable, ce qui entraîne une plus grande variation parmi les individus soumis à moins de compétition. Le but de cette expérience consistait à déterminer si la réaction variable à un environnement compétitif est en partie un effet d'origine génétique. Les parcelles principales comportaient quatre niveaux de compétition : pas de compétition et des zones dégagées de 3,14, 0,75 et 0,03 m^2. Il y avait 10 individus de chaque clone dans chaque parcelle. Les arbres croissaient généralement plus vite à mesure que la dimension des zones dégagées augmentait. Par contre, des zones dégagées de plus de 3,14 m^2 n'ont pas augmenté la croissance la première année. La variation, exprimée sous forme de coefficient de variation, était plus grande chez les arbres soumis à plus de compétition. Le coefficient de variation intraclone n'était pas relié au niveau de compétition.

[Traduit par la Rédaction]

Introduction

Vegetation control can improve the supply of light, water, and (or) nutrients to crops, and in some cases, removal of competing vegetation can reduce the likelihood of frost damage or death (Menzies and Chavasse 1982). Many authors have recorded improved survival and growth of crops after reductions in competition from other species. In particular, Richardson (1993) summarized the effectiveness of competition control in New Zealand's plantations.

Effects of weed competition on crop variability have apparently varied from study to study. Mason (1992) found that weed control improved survival, growth, and uniformity of crops in the central North Island of New Zealand and included these effects in a model of the growth of juvenile radiata pine (*Pinus radiata* D. Don) stands. Several authors, however, have reported that trees subjected to little competition from weeds did not always respond to their favourable environments, resulting in more variation among individuals subjected to less competition than among those enduring intense competition. Wagner et al. (1989) found that young ponderosa pine (*Pinus ponderosa* Dougl. ex Laws.) stem volume became more variable as competition index of herbaceous vegetation decreased, noting that: "Lower leaf area of competitors provided the opportunity for greater tree growth, but did not insure that it would occur."

Kirongo (1996) reported increasing variation among radiata pine trees with decreasing site occupancy by grass in an experiment on the Canterbury plains, where water is scarce during the summer months. Both Wagner et al. (1989) and Kirongo (1996) used graphs to assess variation and compared absolute variation between trees subjected to different levels of competition. Similar patterns of apparent increased variation of tree crops with decreasing competition indices (CI) have been reported by Comeau et al. (1993) for Engelmann spruce (*Picea engelmannii* Parry ex Englm.) and Burton (1993) among Douglas-fir (*Pseudostuga menzeisii* (Mirb.) Franco) seedlings, both in British Columbia.

Wagner et al. (1989) suggested that increased variation with reductions in competition indices resulted from limitations in resources or tree condition at planting that only became apparent after the stresses imposed by competing plants were removed. Comeau et al. (1993) suggested that a more variable scatter of light transmittance with competition index "...probably results from errors inherent in the visual

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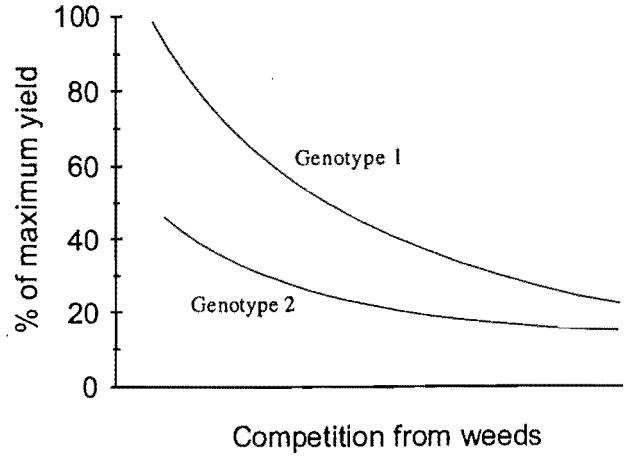
Fig. 1. The hypothesized interaction between genotype and weed competition would involve different patterns of responses to competition, as illustrated by the different responses shown here for genotype 1 and genotype 2.



estimation of percent cover and to the formula used to calculate CI."

Another explanation of increasing variation with decreasing competition could be that it results from a competition × genotype interaction. Different genotypes might have different patterns of response to competition levels (Fig. 1). If this was so, and if an experiment was established with genotype as one factor and level of weed competition as another factor, then the interaction between the two factors would be statistically significant (assuming, of course, that there was adequate power in the experimental design). This paper reports on such a study, where clones of *Pinus radiata* were used to test for different patterns of response to competition among different genotypes.

Using coefficients of variation (CV) to compare variability among treatments when means are different is the standard instruction in textbooks (e.g., Snedecor and Cochran 1989; Huntsberger 1971; Zar 1974). It is expected that variation among entities will increase linearly with increasing average entity size, all other things being equal. This might partly explain the variation observed among trees subjected to less competition in earlier studies, with increases in absolute variation being the natural consequence of increasing plant size. There may, however, be some concern that juvenile trees would not follow the general trend explained in textbooks, with transplanting stress perhaps causing more variation during the first year than during the second, so a comparison of CVs in growth among competition treatments at different ages was conducted in the study reported here.

Coefficient of variation may not be the only feature of a size distribution that is affected by competition. Petersen (1988) found that ponderosa pine was more positively skewed when competing with another species than when it was grown in monoculture.

The objectives of this study were (*i*) to compare variation and skewness of size distributions among trees subjected to different levels of competitive stress in a statistically valid way; (*ii*) to determine whether any observed variable response to competition might be partly a genetic effect, resulting from a genotype × competition interaction; and (*iii*) to examine the effects of differing weed-free spot sizes on growth, survival, and uniformity of radiata pine trees growing on a pastured site in a semiarid environment.

The experiment will also be used in future for detailed studies of the effects of genotype and competition on tree canopy growth and architecture. This paper describes the experimental layout in detail and presents growth and survival results from the first 2 years of measurement.

Materials and methods

An experiment containing seven clones with four levels of weed competition was established on a semiarid site at Dunsandel, on the Canterbury plains of New Zealand during September 1996. The soil was a Lismore stony silt loam, with a cover of mainly Italian ryegrass (*Lolium multiflorum* Lam.) and white clover (*Trifolium repens* L.) but with a large amount of sorrel (*Rumex acetosella* L.). Rainfall averaged 600 mm/year with more falling during the winter than during the summer months. Rainfall was unusually low during the second growing season.

The clones came from controlled pollinated seed, and each of the seven individuals came from a different cross. They were propagated by organogenesis following cryogenic storage of the embryos to retard maturation. After propagation they were hardened off in a nursery, conditioned with an undercutting and wrenching regime, and then sent to the planting site as bare-root plants.

Three complete blocks of four weed control treatments were established on the site. Main plots were 36 × 27 m and contained one of four levels of competition: no competition (9 m^2 of clear ground/tree), 3.14 m^2 cleared spots, 0.75 m^2 spots, and 0.03 m^2 spots. Planting spots were arranged on 3 × 3 m centres. Within each plot there were 10 individuals of each radiata pine clone arranged in lines. These lines were located in the middle of each main plot. Main plots were completely surrounded by a buffer of seedlings subjected to the same levels of pasture competition. Buffer lines were not measured during the study, and so each main plot contained 70 trees that were measured. Lines were ripped to a depth of 30 cm prior to planting.

Weed control was achieved by applying 7.5 kg (all amounts are in units of active ingredients) of terbuthylazine mixed with 300 g of Haloxyfop and 900 g of Clopyralid in 250 L of water per treated hectare 3 weeks after planting. Spot sizes were controlled by placing circular shelters either 2 or 1 m in diameter around trees while they were sprayed. Sorrel was only partly controlled with the above mix, and a subsequent spray during the first summer, which included the addition of 3.75 g of tribenuron methyl and 36 g of oxyfluorfen per treated hectare to the mix, was required to completely control it. The 0.03-m^2 spots were not sprayed a second time. Further spraying late in the second growing season with the same mix was used to clear any weeds that germinated within the treated areas. For future studies, the weed-free areas will be maintained through further herbicide sprays.

Heights and groundline diameters (GLDs) of all individuals of each clone were measured immediately after planting, after 1 year, and again after 2 years. During the first year a few dead trees were replaced using stock set aside for the purpose, but these "blanked" trees were not included in any analyses.

Growth in height and GLD were subjected to analysis of variance (ANOVA) using the general linear models procedure in the SAS package (SAS Institute Inc. 1996). All differences between subsequent measurements of height and GLD were analysed. For hypothesis testing, effects of weed competition were tested against the competition × block interaction, while effects of genotype and genotype × competition were tested against the subplot error term.

Table 1. Height and GLD development in different weed control treatments.

Weed-free area around each tree (m^2)	Height year 0 (cm)	Height growth year 1 (cm)	Height growth year 2 (cm)	GLD year 0 (mm)	GLD growth year 1 (mm)	GLD growth year 2 (mm)	COV GLD growth years 1 and 2	Skewness in GLD growth years 1 and 2
0	20*a*	21*a*	17*a*	5.2*a*	3.9*a*	4.7*a*	45*a*	0.33*a*
0.75	19*a*	27*b*	36*b*	5.2*a*	6.1*b*	12.8*b*	26*ab*	–0.58*b*
3.14	19*a*	34*c*	53*c*	4.7*b*	8.4*c*	19.0*c*	21*b*	–0.59*b*
9	19*a*	32*bc*	67*d*	5.1*ab*	8.8*c*	23.7*d*	19*b*	–0.68*b*

Note: Values in each column with the same letter are not significantly different.

Table 2. *F* values from analyses of variance.

Source	df	Ht0	HG1	HG2	GLD0	GLDG1	GLDG2	Survival
Block (B)	2							
Weed control (WC)	3	0.37	89.52*	85.71*	6.06*	146.15*	164.24*	5.54*
B × WC	6							
Clone (C)	6	38.95*	5.84*	3.83*	16.82*	11.92*	7.04*	6.07*
C × WC	18	0.42	1.52	2.16*	0.87	0.79	1.61	0.8
B × C × WC	49							

*Significant at $P < 0.05$.

Fig. 2. Height growth of individual clones versus weed-free area per tree, showing the interaction between clone and competition (clone 7, in particular responded differently from the other clones).

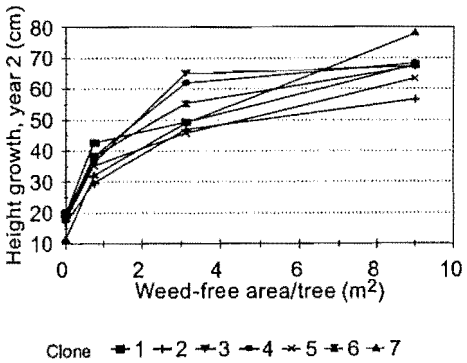
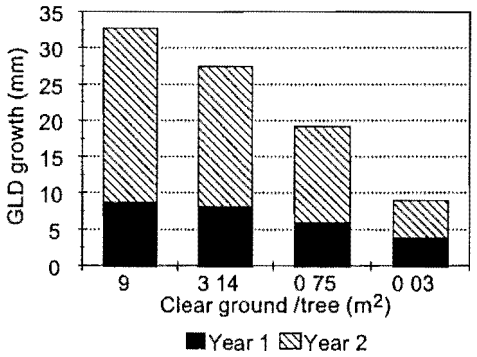


Fig. 3. Groundline diameter growth versus weed-free area per tree. Differences between 3.14 m^2 spots and 9 m^2 of clear area/tree during year 2 were not evident during year 1.



Coefficient of variation of growth in GLD at a subplot level was also subjected to ANOVA but with data obtained after the first and the second year included in the analysis so that any differences in CV between years or interactions between treatments and years could be tested for statistical significance. In addition, skewness of growth in GLD during the first 2 years was calculated for each weed-control treatment. Standard errors for skewness (Sokal and Rohlf 1981) were calculated, and weed control treatments were tested for statistically significant differences in skewness.

Survival within each subplot was transformed with an arcsine square root transformation before analysis.

Results

Results (Tables 1 and 2) showed that there were no interactions between clone and level of competition for any of the dependent variables during the first year or over the first 2 years. However, analysis of year 2 height growth showed that, during this year, some clones exhibited greater height growth differences with competition than others (Fig. 2).

Trees in 3.14 m^2 spots did not grow significantly less in height or GLD during the first year than those subjected to no competition, but both these treatments were significantly different from the 0.75-m^2 spot treatment, which in turn was significantly different from the 0.03-m^2 spot treatment in GLD growth ($P < 0.0001$, Fig. 3). By the end of the second year, however, all four competition treatments were significantly different ($P < 0.0001$) in height growth (Table 1) and GLD growth (Fig. 3). Trees subjected to maximum levels of competition grew significantly ($P < 0.0006$) less in height than those of the other treatments (Table 1). There were also significant differences in both height ($P < 0.0001$) and GLD ($P < 0.0001$) growth among clones.

Weed competition did not significantly affect survival during the first year, but survival after the second year was 75% in the control treatment and 89% in the other weed control treatments ($P < 0.0024$). Clones also differed significantly in mortality ($P < 0.0001$). First-year survival of clone 1 was 81%, compared with more than 90% for all the other clones. By the end of the second year, the 62% survival of

Table 3. Height, GLD development and survival among the seven clones.

Clone	Height year 0 (cm)	Height growth year 1 (cm)	Height growth year 2 (cm)	GLD year 0 (mm)	GLD growth year 1 (mm)	GLD growth year 2 (mm)	COV GLD growth years 1 and 2	Survival years 1 and 2 (%)
3	23*b*	29*ab*	47*a*	5.1*bc*	8.5*a*	25*a*	20*a*	78*ab*
4	21*bc*	32*a*	46*a*	5.0*bc*	6.9*b*	24*ab*	24*a*	95*a*
6	28*a*	27*bc*	45*a*	5.8*a*	6.8*bc*	23*abc*	26*a*	96*a*
5	18*cd*	27*bc*	40*ab*	5.5*ab*	6.8*bc*	21*bcd*	39*a*	93*a*
7	13*e*	30*ab*	43*ab*	4.1*d*	6.3*bc*	21*bcd*	28*a*	89*a*
2	17*cd*	29*abc*	37*b*	4.7*cd*	6.3*bc*	21*cd*	24*a*	84*ab*
1	15*de*	26*c*	45*ab*	4.9*c*	5.9*c*	19*d*	35*a*	62*b*

Note: Values in each column with the same letter are not significantly different ($P > 0.05$).

Table 4. *F* values from analysis of variance of CV in GLD growth during the first 2 years.

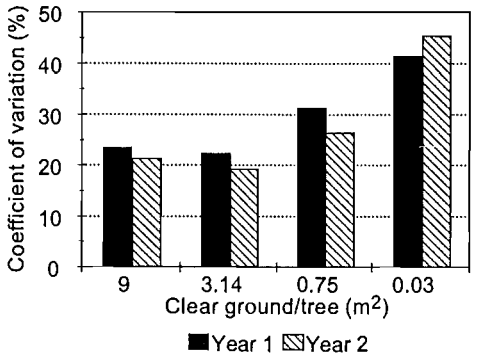
Source	df	*F*
Block (B)	2	
Year (Y)	1	0.32
Weed control (WC)	3	6.4*
WC × Y	3	0.68
B × WC × Y	14	
Clone (C)	6	2.23*
C × Y	6	0.62
C × WC	18	1.01
C × WC × Y	18	0.79
B × C × WC × Y	96	

*Significant at $P < 0.05$.

clone 1 was significantly lower than clones 4, 5, 6, and 7 (Table 3).

Trees subjected to high levels of competition were significantly more variable in growth during both years, as measured by coefficient of variation in GLD growth ($P < 0.001$), than those with little or no competition (Fig. 4). The distribution of GLD growth of trees subjected to the highest level of competition was positively skewed (Table 1), while distributions of trees growing with less competition were negatively skewed ($P < 0.01$). Coefficient of variation did not differ significantly between years (Table 4). There were no significant interactions between year and weed control treatment nor was the interaction between year and clone significant. There was no evidence that trees subjected to less competition failed to respond to their improved microsites (Fig. 5).

Fig. 4. Coefficient of variation in groundline diameter growth during years 1 and 2 versus weed-free area per tree. The CVs did not differ significantly between years.



Discussion

Increasing variation in tree response with reduction in competition reported by Wagner et al. (1989) and Kirongo (1996) did not occur in this experiment. Several possible explanations for this different finding are considered here.

(1) Earlier reports were based on inspections of graphs rather than any explicit, statistically valid tests of variability among treatments with different levels of competition. There may in fact have been no increase in the range of values with decreasing competition in those earlier studies beyond what would have been expected with increasing mean tree size as competition decreased.

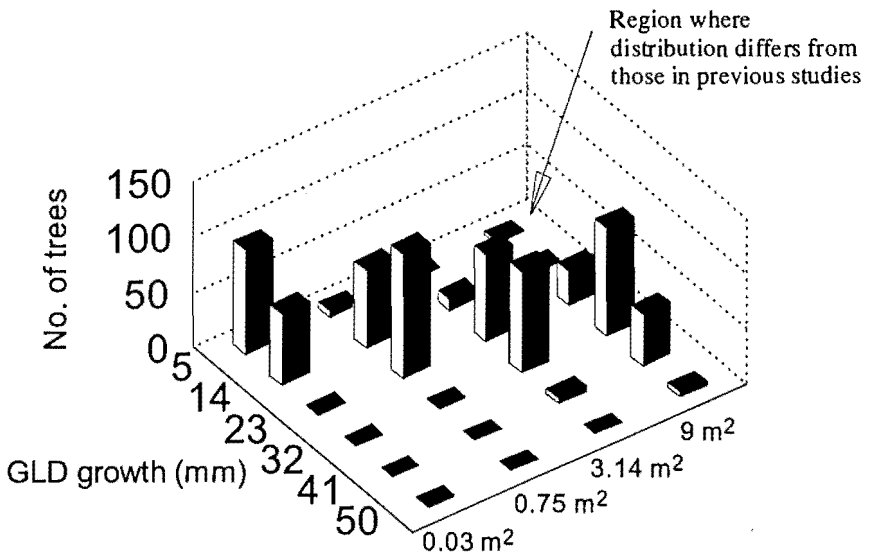
(2) Competition was precisely measured by spot size in the experiment described here, while Wagner et al. (1989), Comeau et al. (1993), Burton (1993), and Kirongo (1996) represented competition by measuring weeds or visually estimating their coverage around individual crop plants. The latter strategy may have resulted in less precise estimates of actual competition, thereby causing an apparent increase in variability with decreasing competition.

(3) The pasture site where this experiment was established may have been less variable than the sites used by other authors.

Option 1 is unlikely. The pattern of response found by Kirongo (1996) contained many points in the lower left-hand region of a graph of growth against level of competition. Given the design of the study reported here, in which genotype was a controlled factor, such a two-dimensional graph would illustrate little. A comparison can be made, however, with a three-dimensional graph (Fig. 5), where it is apparent that the equivalent region of the graph (towards the rear right, arrowed) was not populated. It would be useful if data from previous studies were grouped into CI classes so that the CVs of classes could be tested for statistically significant differences.

Option 2, that CIs may be imprecise measurements of competition, remains a possibility. Previous studies used CIs based on measurements or estimates of coverage of individual weed plants adjacent to crop plants within a fixed zone. Fixed-area zones of measurement for CIs may have been

Fig. 5. GLD growth (over 2 years) distributions versus weed-free area per tree. The arrow shows the area of the graph that should have been populated if there had been an increase in variation with decreasing competition similar to that reported from previous studies.



adequate for small trees, but larger trees may have been increasingly affected by plants outside the zones, which may have been quite variable in their levels of site occupancy. Burton (1993) listed several limitations of competition indices, among them difficulties in measuring functional areas of plants, but he also noted that static measures of plants within zones may be inadequate because the relative sizes and densities of competing plants change. In the experiment reported here, cleared spot sizes remained constant, while dimensions and frequencies of plants within the zones measured in previous studies very likely changed within measurement periods.

Option 3, that the pasture site was more uniform than those used in other studies, may also partly explain the different finding reported here. A delayed onset of competition due to lowered fertility was discussed by Harper (1977) as an explanation of differences in relationships between mean plant weight and density. Grace and Tilman (1990) suggested that measured responses to competition become more "disorderly" as the complexity of interactions between plants rises. With more diverse weed species and more variation in underlying site conditions, responses of individual plants to competition, they postulated, become more unpredictable, resulting in graphical patterns similar to those observed by Wagner et al. (1989), Comeau et al. (1993), Burton (1993), and Kirongo (1996). They wrote that with less diversity in the behaviours of weeds, and a more uniform site, patterns should be similar to those found at Dunsandel.

Despite the small interaction between competition and clone in height growth, there was no evidence to suggest that the pattern of responses of individual trees to release from competition that was observed by Wagner et al. (1989) and Kirongo (1996) were caused by a genotype × competition interaction. Competition affected secondary growth to a greater extent than primary growth, and there was no clone × competition effect on GLD in the experiment reported here. Marked differences in the overall slopes of the responses of clones to competition would have been required for any increase in variability among plants subjected to less competition to have been explained by a genotype × competition interaction.

Weed control markedly affected variation between trees. Not only was growth more variable among trees subjected to more competition from pasture, but the diameter distribution was positively skewed, in agreement with the findings of Petersen (1988). The change in symmetry of distributions implied that the relationship between growth and size was nonlinear. Growth suppression was clearly severe for most but not all of the individual plants in the fully pastured treatment, and this experiment provides an opportunity to explore the issue more thoroughly. A fuller analysis of the relationship between plant size and growth rate will be part of a future study on the site.

Competition from pasture severely limited growth in this experiment, and selection of appropriate cleared spot sizes is a critical decision for forest managers. Previous studies of the effects of spot size (Richardson et al. 1996) have provided a guide for conditions in the central North Island of New Zealand but have also shown that extrapolating from experiments to different types of sites might be dangerous. Differences between prescribed and achieved spot sizes were evident in the central North Island experiments. Creating shields to prevent drift outside the desired spot area for the experiment described here facilitated the creation of prescribed spot diameters. Managers should note that, in environments such as Dunsandel, where water supply is limited during the growing season and pasture fully occupies the site prior to establishment, clearing spots larger than 1 m in diameter will result in extra growth even during the first year and that, by the second growing season, there is evidence from this study that clearing spots larger than 2 m in diameter would result in further growth increases. The extent

to which such larger spot sizes might be financially worthwhile can be estimated appropriately from this experiment after responses have been measured over 4 or 5 years, as long-term monitoring of weed control treatments in Canterbury has shown that they tend to be of type I, with an initial gain in productivity that is not sustained throughout the rotation (Mason and Milne 1999). The experiment will not, however, apply directly to sites where spots have been only temporarily cleared unless an assumption is made that parallelism (Mason 1992) begins as soon as the spots are reinvaded by weeds.

Clearly clone 1 was less well suited to the site than the other clones, at least during the first 2 years. Given that clone embryos had been cool stored and then propagated by organogenesis, there is a chance that the performance of these young plants was influenced by effects of physiological ageing or by differential abilities to produce root systems by different individuals. The likely influences of physiological age will become more apparent when it becomes possible to assess the timing of mature bud setting or initiation of reproductive structures. Until such determinations are made, results attributed to clonal differences in this experiment should be adopted only tentatively. There were differences in initial size between clones (Table 3), and although the correlation between initial size and performance was weak overall, the smaller initial size of clone 1 may have contributed to its poorer performance. Initial GLD has been shown to affect performance both within and between batches of radiata pine seedlings in New Zealand (Mason et al. 1997).

Conclusions

Growth of radiata pine clones was suppressed by pasture grasses up to 1 m from each tree during the first year after planting on a dry site in Canterbury, New Zealand. During the second year after planting, grasses more than 1 m from each tree also contributed to growth suppression, and tree size after 2 years was related to competition intensity by a curved response surface. Competition did not significantly affect tree survival after planting.

Clones varied significantly in both survival and growth rate in height and GLD, but there were no interactions between clone and weed competition during the first year, nor overall during the first 2 years. Analyses of growth during the second year revealed a small clone × competition interaction in height.

Variability in GLD growth, expressed as COV, decreased with the removal of competition. There was no evidence that increases in variability with decreasing weed competition reported by other researchers might be caused by a competition × genotype interaction.

Coefficient of variation in GLD growth was not significantly different between years 1 and 2.

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References

Burton, P.J. 1993. Some limitations inherent to static indices of plant competition. Can. J. For. Res. **23**: 2141–2152.

Comeau, P.G., Braumandl, T.F., and Xie, C.Y. 1993. Effects of overtopping vegetation on light availability and growth of Englemann spruce (*Picea englemannii*) seedlings. Can. J. For. Res. **23**: 2044–2048.

Grace, J.B., and Tilman, D. 1990. Perspectives on plant competition. Academic Press, San Diego.

Harper, J.L. 1977. Population biology of plants. Academic Press, London.

Huntsberger, D.V. 1971. Elements of statistical inference. 2nd ed. Allyn & Bacon, Boston, Mass.

Kirongo, B.B. 1996. Effects of non-crop vegetation on growth and productivity of young radiata pine. M. For. Sc. Thesis, University of Canterbury, Christchurch, N.Z.

Mason, E.G. 1992. Decision-support systems for establishing radiata pine plantations in the central north island of New Zealand. Ph.D thesis, University of Canterbury, Christchurch, N.Z.

Mason, E.G., South, D.B., and Zhao, W. 1997. Performance of *Pinus radiata* in relation to seedling grade, weed control, and soil cultivation in the central North Island of New Zealand. N.Z. J. For. Sci. **26**(1/2): 173–183.

Mason, E.G., and Milne, P.G. 1999. Effects of weed control, fertilization, and soil cultivation on the growth of *Pinus radiata* at midrotation in Canterbury, New Zealand. Can. J. For. Res. **29**: 985–992.

Menzies, M.I., and Chavasse, C.G.R. 1982. Establishment trials on frost-prone sites. N.Z. J. For. **27**(1): 33–49.

Petersen, T.D. 1988. Effects of interference from *Calamagrostis rubescens* on size distributions in stands of *Pinus ponderosa*. J. Appl. Ecol. **25**: 265–272.

Richardson, B. 1993. Vegetation management practices in plantation forests of Australia and New Zealand. Can. J. For. Res. **23**: 1989–2005.

Richardson, B., Davenhill, N., Coker, G., Ray, J., Vanner, A., and Kimberley, M. 1996. Optimising spot weed control: first approximation of the most cost-effective spot size. N.Z. J. For. Sci. **26**(1/2): 265–275.

SAS Institute Inc. 1996. SAS/STAT user's guide, version 6.12 edition. SAS Institute Inc., Cary, N.C.

Snedecor, G.W., and Cochran, W.G. 1989. Statistical methods. 8th ed. Iowa State University Press, Ames.

Sokal, R.R., and Rohlf, F.T. 1981. Biometry. 2nd ed. W.H. Freeman & Co., San Francisco, Calif.

Wagner, R.G., Peterson, T.D., Ross, T.W., and Radosevich, S.R. 1989. Competition thresholds for the survival and growth of ponderosa pine seedlings associated with woody and herbaceous vegetation, New For. **3** (2): 151–170.

Zar, J.H. 1974. Biostatistical analysis. Prentice Hall, Englewood Cliffs, N.J.

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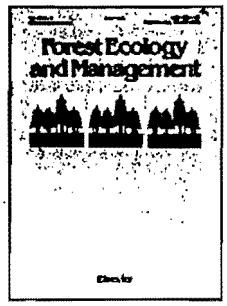

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Dear Dr. Kirongo:

The review of your manuscript, **"Interference mechanisms of pasture on the growth and fascicle dynamics of 3-year old radiata pine clones,"** has been completed and is enclosed for your information. Please prepare a revision along the lines suggested, taking full account of, or rebutting all points made. I will then review the manuscript, and may return it to the reviewers for further comment. Please include an electronic copy of the manuscript and the figures.

I look forward to hearing from you soon. If your revision is not returned within six months, it will be considered as new submission.

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